Systematic Review of Philippine Macaques (Primates, Cercopithecidae: *Macaca fascicularis* subspp.)

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Abstract

Based on study of 352 museum specimens and review of relevant literature, the systematics of Philippine macaques (*Macaca fascicularis*) is examined. Information is presented concerning pelage color, external measurements, cranial characters, blood proteins, and natural history. Two subspecies of Philippine macaques are recognized—*M. f. fascicularis* and *M. f. philippinensis*; between the exclusive ranges of these subspecies is a subspecific contact zone. Subspecific synonymies, type data, distribution summaries, and diagnoses are provided. Zoogeographic hypotheses to account for the present distribution of Philippine macaques are investigated. All known Philippine macaque localities are listed in an annotated gazetteer.

Introduction

The occurrence of monkeys in the Philippine archipelago was revealed to science nearly 300 years ago in separate reports by the English seaman W. Dampier (1697, p. 220) and the German missionary G. J. Camel (in Petiver, 1705, p. 2199). The first known museum specimen, now lost, was sent from Luzon to London in 1837 by H. Cuming (1839, p. 93); on receipt, this specimen was identified by Waterhouse (1838, p. 8) as *Macacus cynomolgus* (= *Macaca fascicularis*). Based on living captives, I. Geoffroy ([1843], p. 568; 1851, pp. 29, 93) attempted to distinguish Philippine macaques from non-Philippine *M. fascicularis*. The first zoologist to work with reasonably adequate series of properly localized specimens from various islands of the archipelago was Mearns (1905, p. 426). Later, Mearns collected additional specimens that were studied by Hollister (1913, p. 328). The treatment of macaques in Taylor's (1934, p. 336) classic review of Philippine mammals essentially follows those of Mearns and Hollister. More recently, Lawrence (1939, p. 62) reported on a small collection of macaques that she obtained in Luzon and Mindoro, and Sanborn (1952, p. 113) briefly reviewed the large collection obtained in six islands in 1946–1947 by H. Hoogstraal, D. S. Rabor, and associates. Additional unreported material, collected principally by D. S. Rabor and associates, has accumulated subsequently. In current checklists, Philippine macaques are routinely allocated to one or two endemic subspecies of *M. fascicularis* (cf. Hill, 1974, p. 522; Napier, 1981, p. 12).

The present review is based on study of 352 specimens of Philippine macaques (Appendix 1) augmented by a survey of relevant literature. Information is available concerning monkeys collected or observed at 154 localities in 29 islands of the archipelago (fig. 1, 154 localities represented by 128 locality symbols; Appendix 2). To establish a broader geographic context for this study, external and cranial characters of Philippine specimens are compared with those of 132 specimens of *M. fascicularis* collected in neighboring Sabah, northern Borneo. Specimens examined are preserved in the following institutions, which hereafter are cited by means of the indicated abbreviations:

AIUZ	Anthropologisches Institut der Universität Zürich, Zurich
AMNH	American Museum of Natural History, New York

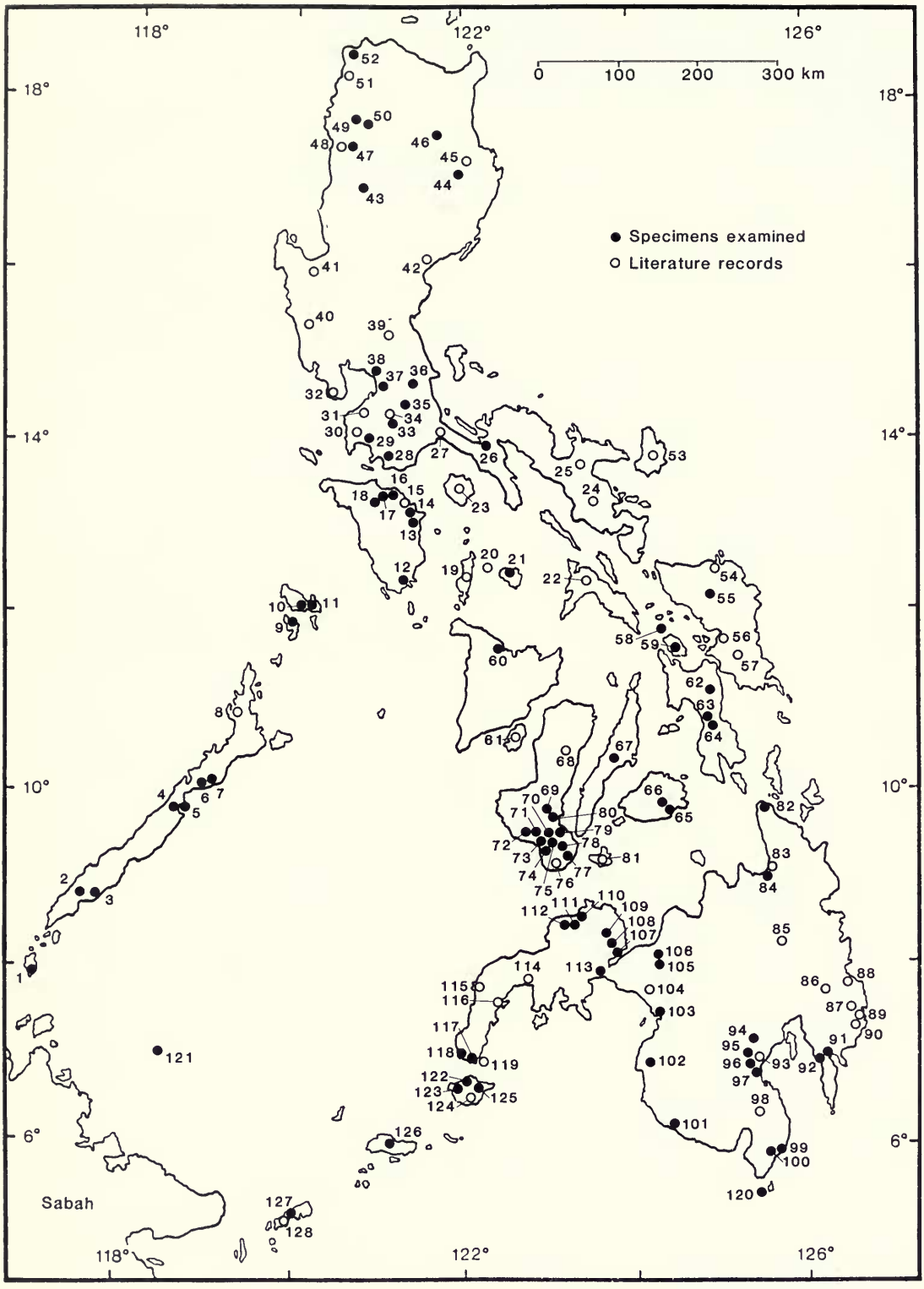

FIG. 1. Known locality records of Philippine *M. fascicularis*. For details, see Gazetteer (Appendix 2). **Key to Locality Numbers**—BALABAC: *1*, Minagas Point. PALAWAN: *2*, Mantalingajan, Mount. *3*, Brookes Point; Macagua. *4*,

BBM	Bernice Bishop Museum, Honolulu (cited for field catalog data only; no Philippine macaque specimens in collection)
BM(NH)	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MMNH	Bell Museum of Natural History, University of Minnesota, Minneapolis
MNHN	Muséum National d'Histoire Naturelle (Mammifères), Paris
NHRM	Naturhistoriska Riksmuseet, Stockholm
PNM	Philippine National Museum, Manila
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
SICONBREC	Simian Conservation, Breeding & Research Center, Inc., Tanay, Luzon, Philippines
SMTD	Staatliches Museum für Tierkunde, Dresden
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
UPLBCF	University of the Philippines at Los Baños, College of Forestry, Los Baños, Luzon, Philippines
UPLBZD	University of the Philippines at Los Baños, Zoology Department, Los Baños, Luzon, Philippines
USNM	National Museum of Natural History, Washington, D.C.
ZMB	Zoologisches Museum des Humboldt-Universität, Berlin

External, Cranial, and Molecular Characters

Pelage Color

Dorsal pelage color in Philippine *M. fascicularis* varies from pale yellowish brown agouti (olivaceous) through golden brown agouti to dark brown agouti (fig. 2). Erythrism is variable. Individual dorsal hairs in the interscapular region of adult

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Lapulapu. *5,* Puerto Princesa; Puerto Princesa area; Puerto Princesa, E; Puerto Princesa, "Mt. wooded area." *6,* Tarabanan. *7,* Malabusog. *8,* Malampaya Sound. CULION: *9,* Makinis; San Pedro. BUSUANGA: *10,* Dimana. *11,* San Nicolas. MINDORO: *12,* Bulalacao. *13,* Pinamalayan. *14,* Pasi. *15,* Naujan Lake National Park. *16,* Calapan. *17,* Alag River. *18,* Halcon, Mount. TABLAS: *19,* Tablas I. ROMBLON: *20,* Romblon I. SIBUYAN: *21,* Guitinguitin, Mount. MASBATE: *22,* Masbate I. MARINDUQUE: *23,* Marinduque I. LUZON: *24,* Albay Prov. *25,* Mount Isarog National Park. *26,* Lopez. *27,* Quezon National Park. *28,* Batangas. *29,* Mahayahaya. *30,* Tuy. *31,* Santa Cruz. *32,* Bataan National Park. *33,* Maquiling, Mount. *34,* Los Baños. *35,* Jalajala. *36,* Daraitan, Mount. *37,* Manila. *38,* Bulacan Prov. *39,* Biak-na-bato National Park. *40,* Zambales Prov. *41,* Pangasinan Prov. *42,* Aurora Memorial Park. *43,* Data, Mount. *44,* Dimalasud Barrio; San Mariano Munic. *45,* Fuyot Spring National Park. *46,* Cagayan Valley. *47,* Barit. *48,* Bessang Pass National Park. *49,* Lagañgilang. *50,* Massisiat. *51,* Laoag. *52,* Nagpartian. CATANDUANES: *53,* Catanduanes I. SAMAR: *54,* Catubig River. *55,* Matuguinao. *56,* San Sebastian. *57,* Sohoton Natural Bridge National Park. MARIPIPI: *58,* Maripipi, 2 km N, 3 km W; Maripipi, 2 km N, 4 km W; Maripipi I. BILIRAN: *59,* Naval, 5 km N, 10 km E; Sayao, Mount. PANAY: *60,* Calantas forest. GUIMARAS: *61,* Guimaras I. LEYTE: *62,* Patoc Barrio. *63,* Baybay, 8.5 km N, 2.5 km E; Pangasugan, Mount. *64,* Balinsasayo Barrio. BOHOL: *65,* Sandayong. *66,* Cantaub. CEBU: *67,* Cebu I. NEGROS: *68,* Canlaon National Park; Canlaon Volcano. *69,* Pagyabonan. *70,* Amio; Naliong. *71,* Kabungahan. *72,* Pamo-at. *73,* Balangbang; Kandomao. *74,* Kauitan. *75,* Inubungan. *76,* Siaton, 10 km N. *77,* Buñga Barrio. *78,* Balinsasayo, Lake; Balinsasayo, Lake, [N bank]; Balinsasayo, Lake, 6 km N and 14 km W of Dumaguete City; Pamplona, 12 km S, 8 km W; Pamplona, 18 km S; Talinis. *79,* Pamplona, near. *80,* Mabaja. SIQUIJOR: *81,* Sequijor I. MINDANAO: *82,* Surigao. *83,* La Union. *84,* Agusan River. *85,* Mainit Hot Spring National Park. *86,* Cateel River and Agusan River, crest between. *87,* Baganga River. *88,* Cateel River, lower. *89,* Caraga. *90,* Manay River. *91,* Kamansi. *92,* Sumlog River. *93,* Parak Creek; Tagulaya River. *94,* McKinley, Mount, E slope, 4800 ft; McKinley, Mount, E slope, 6400 ft. *95,* Apo, Mount; Mainit, Mount Apo, 3800 ft. *96,* Matutungan. *97,* Badiang; Pantod, Mount. *98,* Kibawalan. *99,* Caburan. *100,* Busaw, Mount. *101,* Maculi Point. *102,* Burungkot. *103,* Bugusan. *104,* Camp Vicars–Malabang, between. *105,* Lanao, Lake. *106,* Pantar. *107,* Tangub. *108,* Catagan. *109,* Masawan, Mount Malindang, 3500–4500 ft; Masawan, Mount Malindang, 4400–5000 ft. *110,* Gubat; Libu; Sigayan; Situbo; Tacuta; Tampalan. *111,* Canibongan. *112,* Mamara. *113,* Bucong. *114,* Kabasalan River. *115,* Santa Maria. *116,* Banga, Port. *117,* Pulunbato, Mount; Zamboanga; Zamboanga area. *118,* Ayala; San Ramon. PANGAPUYAN: *119,* Pangapuyan I. BALUT: *120,* Balut I. CAGAYAN SULU: *121,* Cagayan Sulu I. BASILAN: *122,* Isabela. *123,* Camp No. 2–Camp No. 3, between; Camp No. 4–Camp No. 5, between. *124,* Tiputipu. *125,* Basilan I., E end. JOLO: *126,* Crater Lake Mountain, foot. TAWITAWI: *127,* Tawitawi I. *128,* Balimbing.

FIG. 2. Selected standard skins of subadult or adult male Philippine *M. fascicularis*—FMNH 67733 (left), Mindanao: Tacuta (saturation index value, 1.0); FMNH 66348 (center), Negros: Balinsasayo, Lake, N bank (2.0); FMNH 62913 (right), Palawan: Puerto Princesa, E (3.0). Scale bar 10 cm. (Photo by John Weinstein, Division of Photography, FMNH.)

males are 3–5 cm long. Each hair is pale at the root, dark brown over most of its length, and marked subterminally by one or two yellowish to gold bands; the tip of each hair is blackish. In pale specimens, the subterminal bands are broader and paler yellowish than in dark specimens.

The crown is somewhat more brightly colored than the back and usually bears an irregular tuft, crest, or cowlick at the vertex. The anterior edge of the crown is bordered by a blackish superciliary band. Hairs on the side of the head, below the ear, are pale ochraceous gray, elongated, and anteriorly directed; these anteriorly directed subauricular hairs meet the posteriorly directed cheek hairs to form a prominent pale lateral facial crest. The face is thinly haired; facial skin is brown, except for the upper eyelids, which are sharply defined whitish.

On the proximal part of the outer surface of the limbs, pelage is approximately the same color as on the adjacent surface of the trunk; more distally, pelage on the outer surface of the limbs becomes paler—variably gold to yellowish to pale gray at the wrists and ankles. The dorsal surface of the tail is blackish proximally, becoming pale grayish distally. Pelage on the ventral surface of the trunk and tail and on the inner surface of the limbs is thin and pale gray to whitish.

Dorsal pelage color is generally similar in adult males, adult females, and juveniles collected in the same area, but the pelage in adult males is longer and sleeker than in adult females and juveniles. The pelage of young infants (FMNH 33510, 33511; probably less than age 6 months, judging from dental eruption) is fine in texture, blackish dorsally, and grayish ventrally. In older infants (FMNH 66345, 67740, 67741, 75600, 75601; probably age 6–12 months), pelage texture and color approach those in juveniles and adult females.

Paleness or darkness (saturation) of dorsal pel-

TABLE 1. Dorsal pelage color: saturation in Philippine and Sabah *M. fascicularis*.[1]

Island[2]	N	Frequencies (%) at saturation index values					Mean saturation index value
		Pale 1.0	1.5	Intermediate 2.0	2.5	Dark 3.0	
Philippine Islands							
Balabac (*1*)	1					100.0	3.0
Palawan	12				25.0	75.0	2.9
Palawan, S (*3*)	3				33.3	66.7	2.8
Palawan, N (*4–6*)	9				22.2	77.8	2.9
Culion (*9*)	6				83.3	16.7	2.6
Busuanga (*10*)	1			100.0			2.0
Mindoro (*12–14, 16–18*)	7				28.6	71.4	2.9
Luzon	24				16.7	83.3	2.9
Luzon, S (*26, 28, 29, 33, 36, 38*)	12					100.0	3.0
Luzon, N (*43, 44, 46, 47, 49, 52*)	12				33.3	66.7	2.8
Samar (*55*)	3					100.0	3.0
Leyte (*62, 64*)	5					100.0	3.0
Negros, S (*70–75, 77, 78, 80*)	45		6.7	35.6	33.3	24.4	2.4
Mindanao	68	47.1	13.2	19.1	13.2	7.4	1.6
Mindanao, NE (*82, 84*)	2					100.0	3.0
Mindanao, SE (*91, 92, 94–97*)	12		16.7	33.3	33.3	16.7	2.2
Maculi Pt. (*101*)	2				100.0		2.5
Burungkot; Bugusan (*102, 103*)	4	25.0		25.0	25.0	25.0	2.1
Pantar (*106*)	8		25.0	62.5	12.5		1.9
Catagan (*108*)	4	25.0		50.0	25.0		1.9
Bucong (*113*)	5	80.0	20.0				1.1
Katipunan Munic. (*110–112*)	23	78.3	17.4	4.3			1.1
Zamboanga area (*117, 118*)	8	100.0					1.0
Balut (*120*)	1					100.0	3.0
Cagayan Sulu (*121*)	1			100.0			2.0
Basilan (*122, 123, 125*)	3		66.7	33.3			1.7
Tawitawi (*127*)	2	100.0					1.0
ALL	179	19.0	7.8	17.9	21.2	34.1	2.2
Sabah							
Borneo	58	77.6	10.3	12.1			1.2

[1] Excludes infants.

[2] Locality numbers in parentheses (see fig. 1). Intraisland regional data provided for Palawan, Luzon, and Mindanao.

age color in Philippine macaques varies geographically, as previously indicated by Mearns (1905, p. 426), Hollister (1913, p. 328), and Sanborn (1952, p. 113). In order to analyze this variation, I have selected five subadult or adult male skins to serve as standards of comparison. These five skins include two of the palest available Philippine specimens (FMNH 65440, 67733; pale yellowish brown), two of the darkest specimens (FMNH 62913, 87718; dark brown), and one intermediate specimen (FMNH 66348; golden brown). Specimens that match the pale standards have been assigned a saturation index value of 1.0, those that match the intermediate standard have been assigned a value of 2.0, and those that match the dark standards have been assigned a value of 3.0 (fig. 2). Specimens marginal in saturation between the primary standards have been assigned values of 1.5 or 2.5. Infant skins (from specimens that lack permanent teeth) are excluded from this analysis.

Of 14 islands for which postinfant skins are available, 4 are represented exclusively by pale or intermediate specimens (saturation index values 1.0–2.0), 8 are represented exclusively by dark specimens (values 2.5–3.0), and 2 are represented by pale, intermediate, and dark specimens (values 1.0–3.0) (table 1; fig. 3). Islands represented exclusively by pale or intermediate specimens are Tawitawi (N = 2), Cagayan Sulu (1), Basilan (3), and Busuanga (1). Islands represented exclusively by dark specimens are Balabac (1), Palawan (12), Culion (6), Mindoro (7), Luzon (24), Samar (3), Leyte (5), and Balut (1). Islands represented by pale, intermediate, and dark specimens are Mindanao (67) and Negros (45). Within Mindanao, western samples are pale to intermediate, central

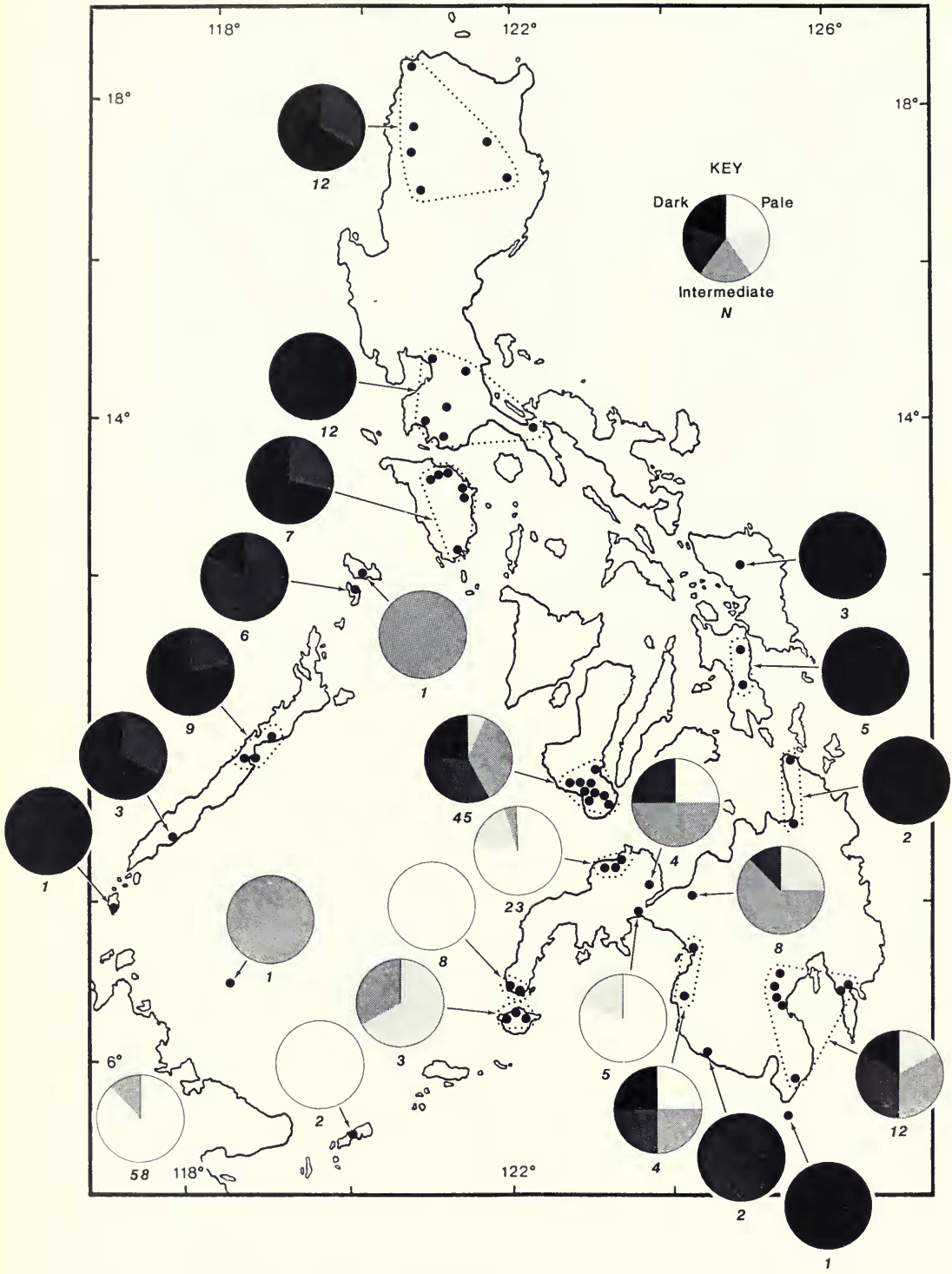

FIG. 3. Geographic variation of dorsal pelage color saturation in samples of Philippine and Sabah *M. fascicularis*. For details, see table 1.

TABLE 2. External measurements (mm) recorded by collectors for adult Philippine *M. fascicularis*. Question marks indicate measurements of doubtful validity.

Island	Loc. no.[1]	N lat.	Head and body length	Tail length	Hind foot length	Ear length
			Females			
Palawan	*2*[2]	8°48′	420	?417	108	30
Busuanga	*11*[2]	12°04′	420	530	115	28
Luzon	*50*[3]	17°35′	?950	515	125	···
	52[4]	18°31′	420	580	131	···
Negros	*71*	9°30′	424, 462	536, 538	118, 130	24, 35
	78	9°21′	400, 410, 433	460, 470, 455	126, 122, 125	26, 27, 29
Mindanao	···[5]	7°30′	420	539	115	29
	103	7°27′	433	564	130	···
	118	7°00′	?370	?570	115	32
	95[6]	6°59′	445, 465	455, 445	128, 120	35, 35
	102[3]	6°52′	430	551	122	···
Tawitawi	*127*	5°10′	394	504	105	31
			Males			
Balabac	*1*[2]	7°54′	?332, 450	544, 510	132, 126	40, 42
Palawan	*5*	9°44′	467, 475	487, 550	132, 136	39, 50
	6[2]	10°01′	530	560	135	43
	7[2]	10°04′	410[7]	510[7]	120[7]	31[7]
Culion	*9*[8]	11°51′	463	496	132	36
	9[9]	11°51′	496, ?563	536, 548	126, 134	38, 36
Busuanga	*10*	12°03′	?381	?595	145	36
Mindoro	*13*	13°02′	450	580	···	50
	14	13°07′	476	552	···	47
	17[10]	13°22′	520	580	140	···
Luzon	*33*	14°08′	500	592	···	···
	36	14°37′	505	510	135	43
	50[3]	17°35′	?1060, ?1080, ?1115	550, 530, 560	140, 145, 140	···
	52[4]	18°31′	500	625	150	···
Leyte	*62*	11°05′	?425	490	130	27
	···[11]	11°00′	?430	?700	135	···
	64	10°40′	?410	590	135	30
Negros	*71*	9°30′	?686	564	140	32
	72	9°30′	466	575	145	36
	70	9°24′	539	578	147	32
Mindanao	*106*[6]	8°04′	500	600	137	39
	94	7°06′	508	536	137	44
	95	6°57′	?575	?425	137	40
	91[3]	6°56′	?390, 490	?615, 585	?292	···
	117[12]	6°54′	445	510	···	···
	102[3]	6°52′	?443	?633	136	39
	97	6°49′	490	531	140	40
Tawitawi	*127*	5°10′	386[6]	507[6]	118[6]	30[6]

[1] See figure 1.
[2] Measurements from field catalog, BBM. [3] Measurements from field catalog, FMNH. [4] Measurements from field catalog, USNM. [5] Zamboanga del Sur Prov. [6] Measurements from Mearns (1905, pp. 429, 430). [7] Abnormally small specimen; measurements excluded from summary statistics. [8] Makinis. [9] San Pedro. [10] Measurements from Hollister (1913, p. 329). [11] Leyte I.; measurements recorded on skull, USNM. [12] Measurements from Martens (1876, p. 206).

and southeastern samples are mixed pale–intermediate–dark, and a small northeastern sample is dark. In summary, available specimens of Philippine *M. fascicularis* are pale to intermediate in the south-central islands of Tawitawi, Cagayan Sulu, and Basilan and in adjacent western Mindanao; they are mixed pale–intermediate–dark in central and eastern Mindanao and in southern Negros; and they are dark elsewhere in the Philippines (except Busuanga, which is represented by one intermediate skin). This pattern of color variation in Philippine *M. fascicularis* does not appear to be closely correlated with climate variation (Djambatan N.V., 1964, p. 10). Fifty-eight skins

TABLE 3. Interisland variation of external measurements (mm) in adult Philippine and Sabah *M. fascicularis*.[1] For details, see table 2.

Island	Head and body length	Tail length	Hind foot length	Ear length
		Females		
Philippine Islands				
Palawan	420	...	108	30
Busuanga	420	530	115	28
Luzon	420	547.5 (2) 515–580	128.0 (2) 125–131	...
Negros	425.8 ± 23.9 (5) 400–462	491.8 ± 41.6 (5) 455–538	124.2 ± 4.5 (5) 118–130	28.2 ± 4.2 (5) 24–35
Mindanao	438.6 ± 17.2 (5) 420–465	510.8 ± 56.3 (5) 445–564	121.7 ± 6.3 (6) 115–130	32.8 ± 2.9 (4) 29–35
Tawitawi	394	504	105	31
ALL	426.9 ± 20.4 (14) 394–465	510.1 ± 45.3 (14) 445–580	120.9 ± 7.8 (16) 105–131	30.1 ± 3.7 (12) 24–35
Sabah				
Borneo[2]	393.3 ± 14.8 (18) 369–420	494.1 ± 29.7 (18) 455–555	116.3 ± 4.1 (18) 108–123	24.8 ± 4.1 (16) 20–35
		Males		
Philippine Islands				
Balabac	450	527.0 (2) 510–544	129.0 (2) 126–132	41.0 (2) 40–42
Palawan	490.7 ± 34.3 (3) 467–530	532.3 ± 39.6 (3) 487–560	134.3 ± 2.1 (3) 132–136	44.0 ± 5.6 (3) 39–50
Culion	479.5 (2) 463–496	526.7 ± 27.2 (3) 496–548	130.7 ± 4.2 (3) 126–134	36.7 ± 1.2 (3) 36–38
Busuanga	...	...	145	36
Mindoro	482.0 ± 35.4 (3) 450–520	570.7 ± 16.2 (3) 552–580	140	48.5 (2) 47–50
Luzon	501.7 ± 2.9 (3) 500–505	561.2 ± 41.8 (6) 510–625	142.0 ± 5.7 (5) 135–150	43
Leyte	...	540.0 (2) 490–590	133.3 ± 2.9 (3) 130–135	28.5 (2) 27–30
Negros	502.5 (2) 466–539	572.3 ± 7.4 (3) 564–578	144.0 ± 3.6 (3) 140–147	33.3 ± 2.3 (3) 32–36
Mindanao	486.6 ± 24.4 (5) 445–508	552.4 ± 38.3 (5) 510–600	137.4 ± 1.5 (5) 136–140	40.4 ± 2.1 (5) 39–44
ALL	487.9 ± 27.1 (19) 445–539	550.7 ± 35.5 (27) 487–625	137.2 ± 6.0 (26) 126–150	39.0 ± 5.9 (22) 27–50
Sabah				
Borneo	451.8 ± 30.8 (18) 400–501	559.8 ± 48.1 (18) 470–650	132.8 ± 8.2 (18) 115–148	29.4 ± 5.7 (18) 22–42

[1] Where insular sample size exceeds two, entries indicate mean ± SD (N) and extremes.
[2] Excludes one abnormally large specimen: FMNH 68700, Kretam Besar, HB = 450 mm.

of *M. fascicularis* collected in Sabah, northern Borneo, are pale to intermediate, matching in saturation the Philippine skins collected in Tawitawi, Cagayan Sulu, Basilan, and western Mindanao. The similarity of pale pelage color in *M. fascicularis* in northern Borneo and Mindanao was previously indicated by Buzeta and Bravo (1850, p. 40).

Erythrism occurs variably in specimens that are pale (USNM 114697, adult male, Mindanao), intermediate (FMNH 66329, adult female, Negros), and dark (FMNH 62902, 62913, USNM 477840, all adult males collected in Palawan). In erythristic specimens, the entire length of each dorsal hair, including both pale and dark segments, is more intensely pigmented than in nonerythristic specimens. Erythrism appears to be somewhat more prevalent in Palawan than in other islands; in Palawan, the color of strongly erythristic specimens tends toward dark chestnut. Sabah specimens av-

TABLE 4. Relative length of tail, hind foot, and ear in various age/sex classes of Philippine *M. fascicularis*: mean ± SD (N).

Age/sex class	Head and body length (mm)	Relative tail length (T/HB × 100)	Relative hind foot length (HF/HB × 100)	Relative ear length (E/HB × 100)
Infants	238.7 ± 48.9 (9)	138.9 ± 21.6 (9)	38.2 ± 4.9 (8)	12.9 ± 1.8 (6)
Juveniles	360.7 ± 40.6 (30)	126.4 ± 10.2 (30)	32.2 ± 2.0 (28)	9.4 ± 1.4 (27)
Subadult females	396.0 ± 6.2 (4)	123.8 ± 19.7 (4)	29.8 ± 1.7 (4)	8.4 ± 0.7 (2)
Subadult males	422.8 ± 41.1 (4)	124.6 ± 6.5 (4)	31.0 ± 4.0 (3)	8.2 ± 1.4 (2)
Adult females	426.9 ± 20.4 (14)	119.6 ± 12.6 (13)	28.4 ± 1.8 (14)	7.0 ± 0.7 (11)
Adult males	487.9 ± 27.1 (19)	113.3 ± 7.8 (19)	27.8 ± 1.6 (14)	8.5 ± 1.3 (14)

erage somewhat less erythristic than Philippine specimens. Albinism is sporadic in Philippine *M. fascicularis* (I. Geoffroy, [1843], p. 568; Sclater, 1875, p. 349; Elera, 1915, p. 34; MNHN 373/265; SICONBREC, living captive observed 4 Aug. 1989).

In a series of three dark brown specimens collected in Samar (FMNH 87717, adult female; 87718, subadult male; 87719, adult female), hair banding is relatively inconspicuous. Tips of the dorsal hairs in all three of these specimens are truncated and frayed. The cause of this unusual truncation and fraying is unknown.

External Measurements

Head and body length (HB) in adult Philippine *M. fascicularis* varies from 394 to 465 mm in 14 females (426.9 ± 20.4 mm, mean ± SD) and from 445 to 539 mm in 19 males (487.9 ± 27.1 mm) (tables 2, 3; cf. Rabor, 1986, p. 138); this excludes measurements of two aberrantly small adult males (SICONBREC 1475, Tawitawi, HB = 386 mm; USNM 477842, Palawan: Malabusog, HB = 410 mm). Relative tail length (T/HB × 100) averages 119.6 in 13 adult females and 113.3 in 19 adult males (table 4). Relative hind foot length (HF/HB × 100) averages 28.4 in 14 adult females and 27.8 in 14 adult males; relative ear length (E/HB × 100) averages 7.0 in 11 adult females and 8.5 in 14 adult males. Weights of wild-collected specimens are known for only one adult female (ca. 4.0 kg) and one adult male (ca. 7.7 kg), both collected at Nagpartian, northern Luzon. Weights of two captive adult females are 3.75 and 3.93 kg (origins—Tawitawi; Mindanao: Zamboanga del Sur), and weights of three captive adult males are 4.25, 5.3, and 7.54 kg (Tawitawi; Leyte; Luzon: Daraitan, Mt.).

Available external measurements of adults are inadequate to establish whether or not head and body length increases with latitude in Philippine *M. fascicularis*; such an increase would be expected in view of the latitudinal increase of greatest skull length (see below). Available measurements also are inadequate to establish whether or not tail length varies geographically in Philippine *M. fascicularis*. Mean head and body length in Philippine *M. fascicularis* exceeds that in Sabah *M. fascicularis* (table 3; *t*-test, $P < 0.001$, females and males); however, overlap between the Philippine and Sabah samples is extensive. Mean relative tail length in Sabah *M. fascicularis* (females, 125.6; males, 124.4) exceeds that in Philippine *M. fascicularis*.

Relative length of the tail, hind foot, and ear all decrease with age in Philippine *M. fascicularis* (table 4). This implies that postnatal growth of these extremities is slower than that of the head and body. The extreme example is postnatal growth of the ear in females, which apparently is negligible from infancy to adulthood.

Cranial Characters (figs. 4, 5)

Greatest skull length (GL) in Philippine *M. fascicularis* varies from 93.7 to 115.8 mm in 75 adult females (105.3 ± 4.3 mm, mean ± SD) and from 109.7 to 139.1 mm in 89 adult males (124.0 ± 5.4 mm) (table 5); this excludes one adult male (BM(NH)) 1876.10.4.9, Luzon: Mahayahaya, GL = 109.3 mm) that is abnormally small compared with other specimens collected in the same area. Relative zygomatic breadth (ZB/GL × 100) averages 65.2 in adult females and 66.0 in adult males (table 6). The rostrum is relatively long and narrow, particularly in adult males; rostral–postrostral ratio (%) averages 49.5 in adult females and 59.0 in adult males. Supramaxillary ridges and lateral maxillary concavities in adults vary from weakly to strongly defined. Canines in adult males are relatively large. A median sagittal crest, formed

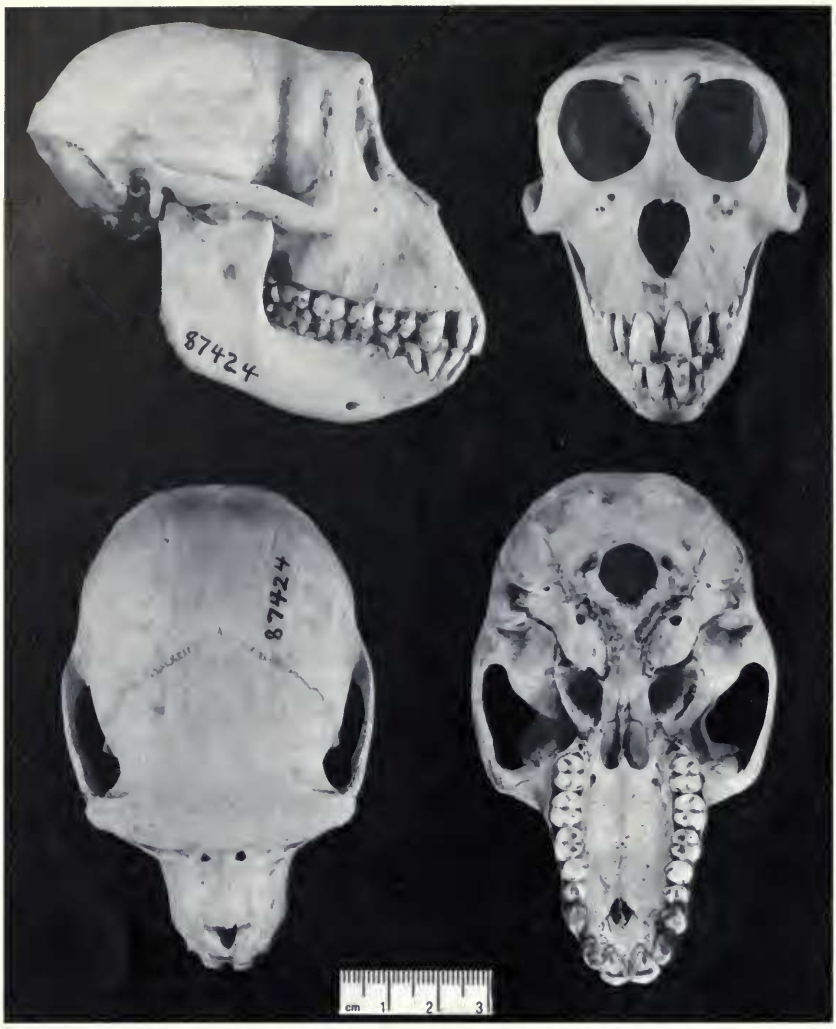

FIG. 4. Skull of adult female Philippine *M. fascicularis*—FMNH 87424, Bohol: Cantaub. (Photos by John Weinstein, Division of Photography, FMNH.)

by progressive ontogenetic convergence of the temporal lines, is prominent in old males.

Skull length in Philippine *M. fascicularis* tends to increase with latitude (figs. 6, 7). Skull length in Sabah *M. fascicularis* averages less than in Philippine *M. fascicularis* (table 5; *t*-test, $P < 0.001$, females and males). However, Sabah means (females, 100.2 mm; males, 116.4 mm; latitude, 5°49′N) are close to values predicted for that latitude by the Philippine *M. fascicularis* regression equations (females, 101.3 mm; males, 120.4 mm) (fig. 7).

Upper molars in *M. fascicularis* frequently bear one or more variably defined accessory entostyles that arise from the lingual cingulum between the protocone and hypocone (fig. 8). Because M^1 is often severely worn, the incidence of accessory entostyles is most conveniently studied in M^2 and M^3 (table 7); the incidence of entostyles in M^3 (0.36, N = 425 teeth) in Philippine and Sabah *M. fascicularis* somewhat exceeds that in M^2 (0.23, N = 575 teeth). In most islands of the Philippine archipelago, the combined incidence of well-defined accessory entostyles in M^2 and M^3 in *M. fascicularis* is less than 0.25. However, in Mindanao (N = 242 teeth) and Mindoro (N = 18 teeth), the incidence is 0.44; the high frequency of accessory entostyles in these two islands was previously noted by Hollister (1913, p. 329). The incidence may also be higher than average in Panay (0.62,

FIG 5. Skull of adult male Philippine *M. fascicularis*—FMNH 67996, Negros: Balangbang. (Photos by John Weinstein, Division of Photography, FMNH.)

N = 8 teeth), Balut (0.50, N = 4), and Basilan (0.38, N = 8), but available samples for these three islands are small. Within Mindanao, the incidence is relatively high (0.41–0.69) in all areas sampled except the Zamboanga area (0.12, N = 8 teeth), extreme southwestern Mindanao, which is represented by a total of only three skulls (table 8). In Sabah *M. fascicularis,* the incidence of accessory entostyles is relatively high (0.39, N = 106), as in Mindanao and Mindoro.

Ontogenetically, growth of the zygomatic arch from infancy to adulthood is approximately isometric with growth of greatest skull length (table 6), as in other macaques. Rostral length (facial skeleton), however, increases allometrically relative to postrostral length (cranial skeleton), also as in other macaques. The power function for the ontogenetic relationship between rostral length (y) and postrostral length (x) determined by the method of reduced major axes is $\log y = 3.725 \log x -$

FIG 6. Size extremes in adult male skulls of Philippine *M. fascicularis*—USNM 125325 (left), Cagayan Sulu, ca. 7°02′N; USNM 144680 (right), Luzon: Nagpartian, 18°31′N. (Photos by Division of Photography, USNM.)

5.456 ($r = 0.917$); 95% confidence limits for the slope are $L_1 = 3.716$ and $L_2 = 3.733$. Ontogenetic development of zygomatic breadth and rostral length in Sabah *M. fascicularis* is similar to that in Philippine *M. fascicularis.*

Blood Proteins

Thirty-two electrophoretic blood-protein loci have been studied in Philippine *M. fascicularis* (Fooden & Lanyon, 1989, p. 211). Of these, 22 loci are essentially fixed in Philippine and non-Philippine *M. fascicularis* (i.e., frequencies of common major alleles are greater than 0.95 in all populations sampled). For the 10 polymorphic loci, allele frequencies in Philippine *M. fascicularis* and non-Philippine *M. fascicularis* are compared in table 9.

Unfortunately, no information is available concerning geographic variation of allele frequencies within the Philippine archipelago, and no blood-protein data from Bornean *M. fascicularis* are available for comparison with Philippine data. Part of the Philippine sample is known to have originated in Mindanao; the island of origin of the balance of this sample is unknown. Because blood-protein data are not available from Bornean *M. fascicularis,* the Philippine sample is compared with a sample of Sumatran *M. fascicularis* and with a composite of all other non-Philippine samples of *M. fascicularis.*

The most striking blood-protein difference between Philippine and non-Philippine *M. fascicularis* is at the Tf locus (for abbreviations, see table 9); in Philippine *M. fascicularis* this locus is monomorphic for allele D, whereas in non-Philippine populations the maximum frequency of allele D is 0.66 (West Malaysia). Philippine *M. fascicularis* also is less variable than non-Philippine *M. fascicularis* at loci Alb (monomorphic), IDH, PGD (monomorphic), and PI. Only locus PHI is notably more variable in Philippine *M. fascicularis* than in non-Philippine *M. fascicularis*; at this locus, allele 5 is relatively frequent (0.17–0.43) in Philippine *M. fascicularis,* whereas it is rare (ca. 0.01)

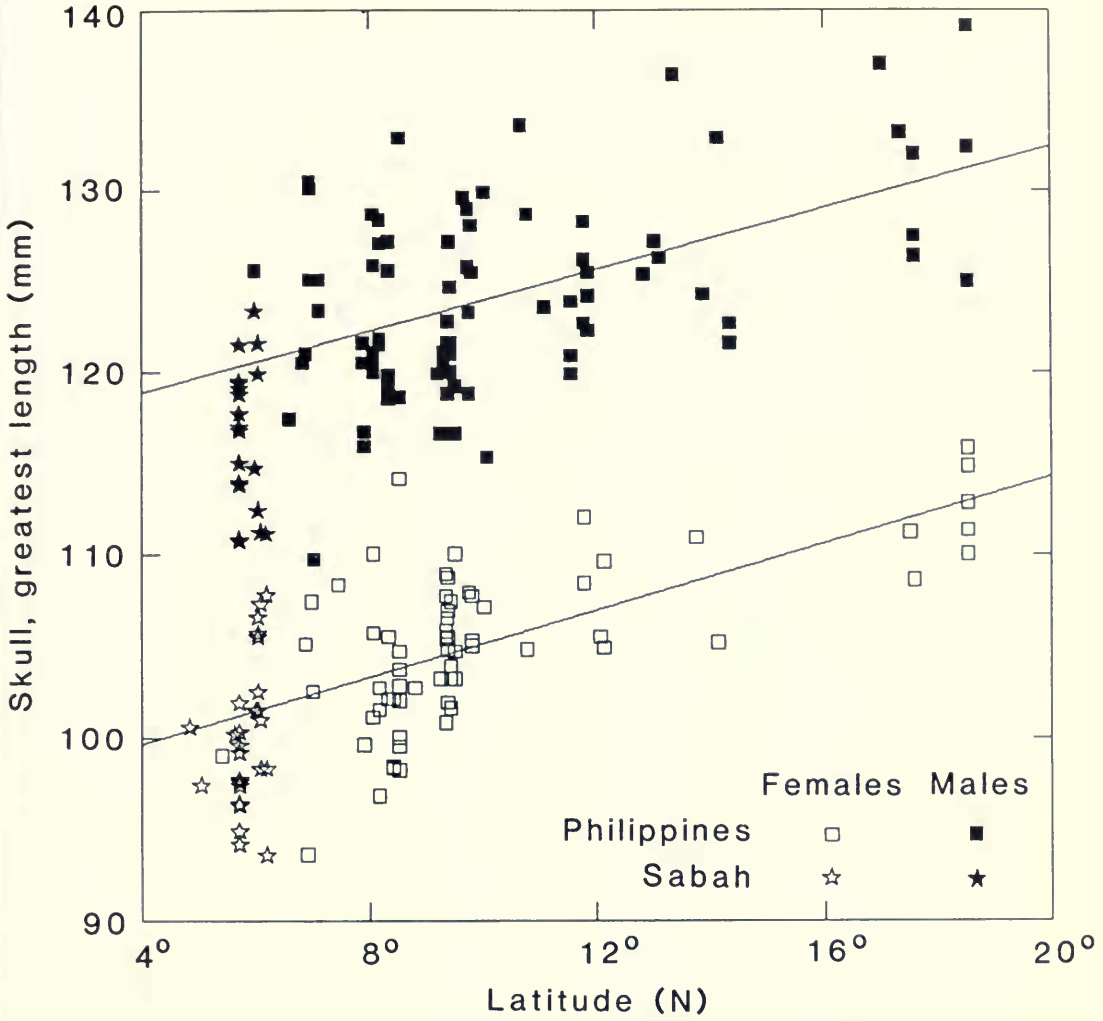

FIG. 7. Latitudinal variation of greatest skull length in adult Philippine and Sabah *M. fascicularis* (cf. table 5). Regression lines indicated for Philippine data (females, slope = 0.91 ± 0.27 [95% confidence limits], *y*-intercept = 96.0, $r = 0.649$; males, slope = 0.85 ± 0.33, *y*-intercept = 115.5, $r = 0.498$).

in non-Philippine *M. fascicularis*. The tendency for blood-protein loci that are variable elsewhere to become fixed in Philippine *M. fascicularis* and in other insular macaques has been noted previously (Goodman et al., 1965, p. 886; Ishimoto, 1973, p. 12; Darga et al., 1975, p. 809; Nozawa et al., 1977, p. 24).

Natural History

Macaca fascicularis is widespread in the Philippine archipelago (fig. 1). Isolated islets as small as 22 km² are known to support viable populations (Balut; Maripipi; Romblon). Islands in the archipelago that possibly or probably are not inhabited by *M. fascicularis* are Batan, 200 km N of Luzon; Dinagat and Siargao, 25 km NE of Mindanao; and Manuk Manka, 25 km S of Tawitawi (for details, see Gazetteer, Appendix 2). Prior to about 1960, the abundance of Philippine *M. fascicularis* was generally reported to be high, but subsequent trapping activities and forest clearance have drastically reduced populations (Cabrera, 1973, p. 252; Rabor, 1977, p. 35).

The habitats in which Philippine *M. fascicularis* has been observed are extremely diverse, ranging from the seashore to oak–pine montane forest at

TABLE 5. Cranial measurements (mm): insular, latitudinal, and local variation in adult Philippine and Sabah *M. fascicularis*.[1]

Island	Loc. no.[2]	N lat.	Greatest length	Zygomatic breadth	Postrostral length	Rostral length
			Females			
Philippine Islands						
Palawan	...	...	104.9 (2)	67.2 (2)	75.9 (2)	36.5 (2)
	2	8°48′	102.7	67.8	74.7	35.1
	6	10°01′	107.1	66.6	77.1	37.8
Busuanga	*11*	12°04′	105.5	72.5	74.0	38.9
Luzon	...	...	111.2 ± 3.2 (9)	69.0 ± 1.4 (9)	79.1 ± 3.6 (9)	40.4 ± 2.3 (9)
			105.2–115.8	67.2–71.3	75.1–87.2	36.8–43.9
	28	13°45′	110.9	69.4	76.2	40.9
	33	14°08′	105.2	71.3	75.6	36.8
	46	17°25′	111.2	68.2	78.7	41.2
	50	17°35′	108.6	68.4	75.1	41.3
	52	18°31′	112.9 ± 2.4 (5)	68.7 ± 1.5 (5)	81.2 ± 3.4 (5)	48.8 ± 2.5 (5)
			110.0–115.8	67.2–70.5	78.5–87.2	37.7–43.9
Samar	*55*	12°08′	107.3 (2)	66.6 (2)	76.3 (2)	39.0 (2)
			104.9–109.6	65.6–67.5	76.0–76.6	35.4–42.5
Maripipi	*58*	11°47′	110.2 (2)	68.7 (2)	76.7 (2)	44.0 (2)
			108.4–112.0	67.9–69.5	76.3–77.2	41.5–46.5
Leyte	*63*	10°46′	104.8	67.5	75.8	36.5
Bohol	...	...	106.5 ± 1.5 (4)	66.3 ± 1.6 (4)	75.3 ± 0.5 (4)	39.2 ± 1.6 (4)
			105.0–107.9	64.5–68.2	74.6–75.9	37.3–41.1
	66	9°48′	106.0 ± 1.5 (3)	65.6 ± 1.3 (3)	75.3 ± 0.6 (3)	39.1 ± 1.9 (3)
			105.0–107.7	64.5–67.0	74.6–75.9	37.3–41.1
	65	9°45′	107.9	68.2	75.3	39.7
Negros	...	...	105.3 ± 2.6 (19)	70.7 ± 1.7 (19)	74.8 ± 1.7 (19)	37.4 ± 2.3 (19)
			100.8–110.0	68.0–73.7	71.7–79.1	34.0–42.6
	71	9°30′	106.6 (2)	71.2 (2)	76.0 (2)	38.4 (2)
			103.2–110.0	68.8–73.7	72.8–79.1	37.6–39.1
	79	9°30′	104.7	72.4	76.0	35.4
	70[3]	9°26′	104.0 ± 2.4 (4)	69.7 ± 1.7 (4)	74.8 ± 0.3 (4)	36.8 ± 1.7 (4)
			101.6–107.4	68.0–71.7	74.4–75.0	35.1–39.1
	78[4]	9°23′	104.4 (2)	70.5 (2)	74.5 (2)	36.0 (2)
			101.9–106.9	68.1–72.9	73.1–75.8	35.7–36.2
	75	9°23′	106.3 ± 2.1 (3)	70.3 ± 1.6 (3)	75.9 ± 0.7 (3)	38.3 ± 1.7 (3)
			104.8–108.7	69.0–72.1	75.2–76.6	36.8–40.2
	78[5]	9°22′	107.7 (2)	71.7 (2)	73.3 (2)	41.1 (2)
			106.5–108.9	70.3–73.0	72.2–74.3	39.5–42.6
	78[6]	9°21′	104.9 ± 2.9 (4)	70.7 ± 0.9 (4)	74.1 ± 1.6 (4)	37.3 ± 2.9 (4)
			100.8–107.7	69.6–71.7	71.7–75.0	34.3–41.1
	...[7]	9°15′	103.2	72.1	74.8	34.0
Mindanao	...	...	102.6 ± 4.4 (25)	68.4 ± 2.5 (26)	75.0 ± 2.6 (25)	35.7 ± 2.8 (26)
			93.6–114.1	63.6–73.6	71.3–82.8	30.7–41.0
	110[8]	8°31′	108.5 (2)	73.1 (2)	77.8 (2)	40.1 (2)
			102.8–114.1	72.5–73.6	72.8–82.8	39.2–41.0
	110[9]	8°31′	104.7	68.3	75.7	37.5
	110[10]	8°31′	100.0	66.0	75.3	35.5
	110[11]	8°31′	100.5 ± 2.9 (3)	68.6 ± 1.2 (3)	74.7 ± 1.2 (3)	34.6 ± 3.0 (3)
			98.2–103.7	67.5–69.8	73.5–75.9	31.6–37.5
	110[12]	8°31′	102.0	73.2	73.7	35.5
	111	8°25′	98.3	67.8	72.3	33.1
	112	8°25′	100.3 (2)	65.0 (2)	73.1 (2)	33.8 (2)
			98.4–102.1	63.6–66.4	72.5–73.7	32.2–35.3
	109	8°20′	103.8 (2)	67.4 (2)	75.6 (2)	35.4 (2)
			102.1–105.5	66.5–68.3	74.5–76.7	34.5–36.2
	108	8°10′	100.3 ± 3.1 (3)	66.7 ± 1.0 (3)	74.9 ± 2.5 (3)	34.1 ± 2.7 (3)
			96.8–102.7	65.6–67.4	72.2–77.2	32.2–37.2
	106	8°04′	107.9 (2)	68.7 (2)	76.3 (2)	40.1 (2)
			105.7–110.0	67.7–69.6	75.4–77.1	39.1–41.0

TABLE 5. Continued.

Island	Loc. no.[2]	N lat.	Greatest length	Zygomatic breadth	Postrostral length	Rostral length
	107	8°03′	101.1	68.7	71.8	36.0
	113	7°54′	99.6	68.2	73.5	33.8
	103	7°27′	108.3	68.8	77.7	36.6
	118	7°00′	102.5	70.2	74.6	35.1
	95	6°59′	107.4	70.7 (2)	79.1	36.6 (2)
				70.0–71.4		33.5–39.6
	117	6°54′	93.6	64.3	71.3	30.7
Balut	*120*	5°24′	99.0	63.8	71.9	33.8
Unknown	...	...	106.0 ± 2.4 (9)	66.5 ± 1.7 (9)	...	...
			103.0–109.6	64.4–69.3		
ALL	...	...	105.3 ± 4.3 (75)	68.6 ± 2.5 (76)	75.6 ± 2.7 (66)	37.4 ± 3.2 (67)
			93.6–115.8	63.6–73.7	71.3–87.2	30.7–46.5
Sabah						
Borneo[13]	...	5°49′[14]	100.2 ± 3.8 (28)	65.9 ± 3.6 (28)	73.2 ± 2.5 (26)	33.6 ± 2.4 (26)
			93.6–107.8	59.4–72.5	69.4–77.8	29.9–39.0
			Males			
Philippine Islands						
Balabac	*1*	7°54′	116.3 (2)	80.6 (2)	79.5 (2)	44.7 (2)
			115.9–116.7	80.4–80.8	79.0–79.9	44.6–44.7
Palawan	...	...	123.4 ± 6.9 (5)	81.5 ± 5.0 (5)	83.3 ± 4.5 (4)	51.5 ± 2.9 (4)
			115.3–129.9	75.8–88.5	76.7–86.4	47.4–53.6
	5	9°44′	127.4 (2)	82.7 (2)	85.0 (2)	52.6 (2)
			125.8–129.0	82.0–83.3	83.8–86.1	51.6–53.6
	6	10°01′	129.9	88.5	86.4	53.5
	7	10°04′	115.3	77.8	76.7	47.4
	?	...	116.8	75.8	...	...
Culion	...	...	124.0 ± 1.6 (3)	82.8 ± 2.1 (3)	82.6 ± 2.9 (3)	48.0 ± 1.7 (3)
			122.3–125.5	81.2–85.1	80.1–85.8	46.2–49.4
	9[15]	11°51′	122.3	82.0	80.1	48.5
	9[16]	11°51′	124.9 (2)	83.2 (2)	83.9 (2)	47.8 (2)
			124.2–125.5	81.2–85.1	82.0–85.8	46.2–49.4
Mindoro	...	...	128.8 ± 5.1 (4)	82.3 ± 3.5 (4)	86.7 ± 1.8 (4)	51.1 ± 3.2 (4)
			125.4–136.4	77.2–85.1	84.8–89.2	46.7–54.2
	13	13°02′	127.2	77.2	84.8	52.6
	14	13°07′	126.3	83.8	86.8	50.9
	17	13°22′	136.4	85.1	89.2	54.2
	?	...	125.4	83.0	86.1	46.7
Luzon[17]	...	...	129.5 ± 5.7 (12)	81.3 ± 3.6 (12)	87.7 ± 3.0 (7)	53.0 ± 2.8 (7)
			121.6–139.1	74.8–88.6	84.3–92.2	48.9–55.8
	26	13°53′	124.3	77.8	...	...
	33	14°08′	132.9	80.1	85.4	54.2
	35	14°21′	122.2 (2)	80.4	...	...
			121.6–122.7			
	44	17°00′	137.0	85.9	90.1	55.8
	47	17°20′	133.2	82.2	...	...
	50	17°35′	128.6 ± 3.0 (3)	80.2 ± 0.9 (3)	85.5 ± 1.3 (3)	50.7 ± 2.6 (3)
			126.4–132.0	79.1–80.9	84.3–86.9	48.9–53.6
	52	18°31′	132.2 ± 7.1 (3)	82.0 ± 6.9 (3)	91.1 (2)	54.4 (2)
			125.0–139.1	74.8–88.6	89.9–92.2	52.9–55.8
	?	...	...	82.9	...	...
Maripipi	*58*	11°47′	125.7 ± 2.8 (3)	82.4 ± 1.9 (4)	83.8 ± 1.7 (3)	51.3 ± 1.7 (4)
			122.7–128.3	79.5–83.5	81.9–84.9	49.8–53.4
Biliran	*59*	11°33′	123.9	82.1	83.7	49.1
Panay	*60*	11°33′	120.4 (2)	82.0 (2)	81.9 (2)	47.7 (2)
			119.9–120.9	81.5–82.5	81.8–81.9	46.9–48.4

TABLE 5. Continued.

Island	Loc. no.[2]	N lat.	Greatest length	Zygomatic breadth	Postrostral length	Rostral length
Leyte	...	...	128.8 ± 4.1 (4)	82.2 ± 1.6 (4)	85.8 ± 2.1 (4)	51.2 ± 3.2 (4)
			123.6–133.6	80.6–83.8	83.0–88.2	47.2–54.1
	62	11°05′	123.6	80.6	83.0	47.2
	63	10°46′	128.7	83.8	85.7	50.0
	64	10°40′	133.6	83.3	88.2	54.1
	?	...	129.4	81.2	86.3	53.4
Bohol	...	...	125.6 ± 2.4 (3)	80.5 ± 2.4 (3)	83.5 ± 1.9 (3)	51.1 ± 0.9 (3)
			123.3–128.1	79.1–83.2	82.0–85.7	50.2–51.9
	66	9°48′	125.5	79.1	82.8	51.9
	65	9°45′	123.3	79.1	82.0	50.2
	?	...	128.1	83.2	85.7	51.2
Negros	...	...	121.4 ± 3.6 (15)	83.1 ± 2.3 (15)	81.8 ± 1.7 (15)	47.8 ± 2.2 (15)
			116.6–129.6	79.6–87.8	79.6–84.9	44.0–52.4
	80	9°39′	129.6	84.8	84.9	52.4
	71	9°30′	116.6	81.1	79.6	44.7
	72	9°30′	119.2	82.9	81.2	46.3
	70[3]	9°26′	120.8 (2)	81.8 (2)	81.3 (2)	48;0 (2)
			120.0–121.6	79.6–84.0	81.0–81.5	46.7–49.2
	73[18]	9°25′	122.9 (2)	84.2 (2)	83.6 (2)	48.3 (2)
			121.0–124.7	83.4–84.9	82.8–84.4	48.0–48.5
	70[19]	9°24′	127.2	85.7	84.3	49.9
	78[4]	9°23′	122.2 (2)	82.6 (2)	80.9 (2)	48.3 (2)
			121.6–122.8	80.8–84.4	80.7–81.1	48.2–48.4
	73[20]	9°23′	118.8	83.4	80.0	45.7
	74	9°18′	121.1	81.4	81.3	49.9
	78[21]	9°18′	120.6	87.8	83.2	47.8
	...[7]	9°15′	116.6	81.6	79.6	44.0
	77	9°12′	119.9	80.0	82.0	47.3
Mindanao	...	...	123.6 ± 4.2 (26)	82.3 ± 2.3 (26)	82.9 ± 2.7 (25)	48.7 ± 2.8 (25)
			118.5–132.9	77.8–85.9	78.9–90.8	42.5–54.4
	82	9°45′	118.8	84.8	...	...
	110[8]	8°31′	118.6	82.6	81.0	46.8
	110[11]	8°31′	132.9	84.6	90.8	51.5
	109	8°20′	122.0 ± 4.0 (5)	80.5 ± 1.7 (5)	82.3 ± 2.7 (5)	46.6 ± 3.3 (5)
			118.5–127.2	78.3–82.4	78.9–85.3	42.5–51.0
	108	8°10′	124.7 ± 3.6 (4)	83.0 ± 0.7 (4)	83.0 ± 2.3 (4)	49.8 ± 1.3 (4)
			121.5–128.4	82.4–83.9	81.0–85.5	48.2–51.4
	106	8°04′	121.9 ± 2.7 (4)	81.2 ± 2.1 (4)	82.3 ± 2.0 (4)	47.1 ± 2.5 (4)
			120.0–125.9	78.1–82.7	79.9–84.7	45.0–50.5
	107	8°03′	128.7	84.2	82.1	54.4
	105	7°53′	121.1 (2)	80.5 (2)	81.2 (2)	47.9 (2)
			120.5–121.6	80.3–80.7	80.5–81.9	47.1–48.6
	94	7°06′	124.3 (2)	84.2 (2)	82.8 (2)	49.3 (2)
			123.4–125.1	82.8–85.5	82.3–83.3	47.5–51.0
	95	6°57′	130.1	84.9	86.5	51.4
	91	6°56′	127.8 (2)	85.5 (2)	85.8 (2)	50.9 (2)
			125.1–130.5	85.1–85.9	85.3–86.2	48.9–52.9
	102	6°52′	121.0	81.4	80.0	48.1
	97	6°49′	120.5	77.8	80.9	48.3
Cagayan Sulu	*121*	7°01′	109.7	77.5	75.0	43.9
Basilan[22]	*125*	6°35′	117.4	81.3	80.1	44.7
Jolo	*126*	5°58′	125.6	89.9	87.2	47.4
Unknown	...	...	120.5 ± 4.8 (6)	76.3 ± 3.4 (6)	...	...
			114.9–128.3	71.5–79.6		
ALL	...	...	124.0 ± 5.4 (89)	81.8 ± 3.2 (90)	83.4 ± 3.2 (76)	49.2 ± 3.1 (77)
			109.7–139.1	71.5–89.9	75.0–92.2	42.5–55.8
Sabah						
Borneo	...	5°49′[14]	116.4 ± 4.0 (20)	80.0 ± 3.6 (20)	79.8 ± 2.7 (20)	44.2 ± 3.0 (20)
			110.7–123.4	74.3–87.9	75.7–85.7	38.2–47.6

TABLE 6. Cranial measurements and ratios in various age/sex classes of Philippine *M. fascicularis*: mean ± SD (N).

Age/sex class	Greatest length (mm)	Relative zygomatic breadth (ZB/GL × 100)	Postrostral length (mm)	Rostral-postrostral ratio (R/PR × 100)
Infants	77.3 ± 4.9 (15)	64.5 ± 2.9 (15)	65.5 ± 3.0 (15)	27.1 ± 3.7 (15)
Juveniles	96.6 ± 9.1 (98)	63.9 ± 2.2 (97)	73.2 ± 4.2 (75)	41.3 ± 6.0 (75)
Subadult females	101.4 ± 4.8 (12)	64.4 ± 3.1 (12)	75.8 ± 3.1 (10)	45.5 ± 2.0 (10)
Adult females	105.3 ± 4.3 (75)	65.2 ± 2.9 (75)	75.6 ± 2.7 (66)	49.5 ± 3.7 (66)
Subadult males	114.5 ± 6.3 (20)	65.6 ± 3.4 (20)	80.3 ± 3.0 (17)	54.5 ± 3.2 (17)
Adult males	124.0 ± 5.4 (89)	66.0 ± 2.8 (88)	83.4 ± 3.2 (76)	59.0 ± 2.7 (76)

TABLE 7. Accessory entostyles: frequency in Philippine and Sabah *M. fascicularis*.

	RM^2		RM^3		LM^2		LM^2		Total		
Island	N	With styles	N	With styles	N	With styles	N	With styles	N	With styles	Frequency
Philippine Islands											
Balabac	4	0	4	1	4	0	4	1	16	2	0.12
Palawan	11	1	8	2	10	2	7	1	36	6	0.16
Culion	4	0	3	0	4	0	3	0	14	0	0.00
Busuanga	1	0	1	0	1	0	1	0	4	0	0.00
Mindoro	5	1	4	3	5	2	4	2	18	8	0.44
Luzon	26	1	18	4	26	5	18	4	88	14	0.16
Sibuyan	1	0	0	...	1	0	0	...	2	0	0.00
Samar	3	0	3	1	3	0	3	1	12	2	0.17
Maripipi	9	1	6	3	9	0	5	1	29	5	0.17
Biliran	0	...	0	...	1	0	1	1	2	1	0.50
Panay	2	1	2	2	2	0	2	2	8	5	0.62
Leyte	9	0	6	1	8	0	6	1	29	2	0.07
Bohol	9	0	8	0	8	0	8	0	33	0	0.00
Negros	48	6	38	11	48	3	38	6	172	26	0.15
Mindanao	67	25	54	24	67	29	54	28	242	106	0.44
Balut	1	0	1	1	1	0	1	1	4	2	0.50
Cagayan Sulu	1	0	1	0	1	0	1	0	4	0	0.00
Basilan	2	1	2	2	2	0	2	0	8	3	0.38
Jolo	1	0	1	0	1	0	1	0	4	0	0.00
ALL	204	37	160	55	202	41	159	49	725	182	0.25
Saban											
Borneo	84	29	53	24	85	27	53	26	275	106	0.39

←

[1] Where sample size exceeds two, entries indicate mean ± SD (N) and extremes. For explanation of measurements, see Fooden (1969, p. 41).

[2] See figure 1.

[3] Naliong. [4] Balinsasayo, Lake, [N bank]. [5] Balinsasayo, Lake, 6 km N and 14 km W of Dumagete City. [6] Talinis. [7] Negros I., S. [8] Gubat. [9] Libu. [10] Sigayan. [11] Situbo. [12] Tampalan. [13] Excludes one abnormally large specimen: FMNH 68700, Kretam Besar, GL = 115.8 mm. [14] Mean latitude of Sabah: Borneo localities. [15]Makinis. [16] San Pedro. [17] Excludes one abnormally small specimen: BM(NH) 1876.10.4.9, Mahayahaya, GL = 109.3 mm. [18] Balangbang. [19] Amio. [20] Kandomao. [21] Pamplona, 18 km S. [22] A second Basilan specimen (USNM 144665) listed by Hollister (1913, p. 330) as an adult actually is a subadult.

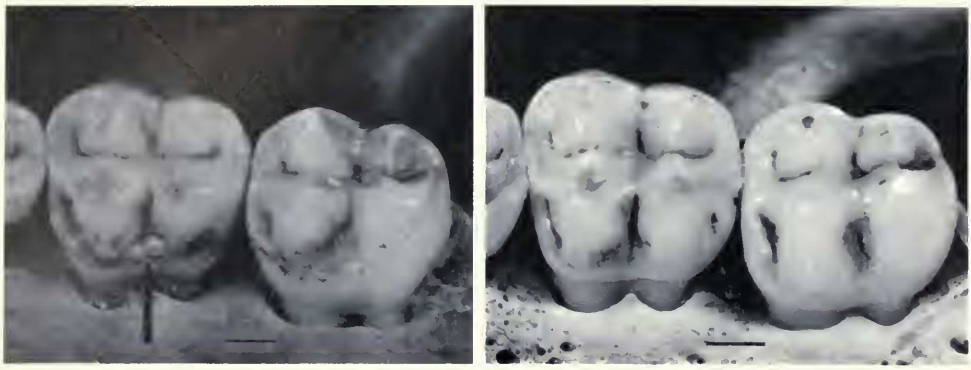

FIG. 8. Accessory entostyle variation in Philippine *M. fascicularis,* lingual view of left M^{2-3}—FMNH 62905 (left), male, Palawan: Puerto Princesa, pair of large entostyles present on M^2 (arrow) and smaller entostyles present on M^3; FMNH 87424 (right), female, Bohol: Cantaub, entostyles weakly defined or absent. Scale bar 2 mm. (Photos by John Weinstein, Divison of Photography, FMNH.)

2300 m altitude (table 10). The frequent occurrence of *M. fascicularis* in primary evergreen rain forest in the Philippines is particularly notable, because this habitat is rarely occupied by *M. fascicularis* in Borneo, Sumatra, and peninsular Malaysia (Fooden, 1982, p. 574). Although Philippine *M. fascicularis* is often seen on the ground, it probably spends most of its waking hours in trees and typically takes to the trees when alarmed (La Gironiere, [1853?], p. 193; Rabor, 1955, p. 211; 1977, p. 238; 1986, p. 138; FMNH 62915, field note). Its arboreal locomotion is agile and includes leaps of 5–7 m between branches. At night it sleeps in groups in roosting trees (FMNH 62914, field note).

Fruit apparently is the main food of Philippine *M. fascicularis* (Rabor, 1955, p. 210; 1977, p. 238; 1986, p. 138; L. R. Heaney, FMNH, field notes, Leyte). The diet also is known to include animal food, such as pigeons (*Ducula* sp.; FMNH 62906, field note), lizards and earthworms (Alcala, 1976, p. 145), and oysters and crabs, which are taken along the seashore (Günther, [1877], p. 735; E. A. Mearns, unpubl. MS., USNM). Insects and birds' eggs presumably are also eaten; monkeys have been observed on the forest floor searching for food—presumably arthropods—under rocks and branches (L. R. Heaney, FMNH, field notes, Leyte). Cultivated crops are often raided; these include maize, sweet potatoes (camote), turnips, bananas, papayas, ube, and gabi (La Gironiere, [1853?], p. 193; Slack, 1867, p. 37; Whitehead in Thomas, 1898, p. 381; Rabor, 1977, p. 239; 1986, p. 138; E. A. Mearns, unpubl. MS., USNM; L. R. Heaney, FMNH, field notes, Leyte; FMNH 56995, note). The only reported nonhuman predator on this monkey is the large endemic Philippine eagle *Pithecophaga jefferi* (Ogilvie Grant, 1897, p. 219; Whitehead, 1899, p. 91; Clemens, 1907, p. 93; Gonzales, 1968, p. 482; Rabor, 1977, p. 35; Kennedy, 1977, p. 5; 1981, p. 853). Rabor (1977, p. 35) asserts that *M. fascicularis* was the principal food of this eagle before recent decimation of monkey populations, but Gonzales (1968, p. 482) and Kennedy (1981, p. 853) indicate that flying lemurs, *Cynocephalus volans,* are the eagle's preferred prey, even where monkeys are abundant.

Only seven estimates of troop size are available; these are 5–10 (Biliran; Rickart et al., in prep.), 5–10 (Maripipi, Rickart et al., in prep.), 6–12 (Rabor, 1986, p. 138), 12 (E. A. Mearns, unpubl. MS., USNM), as many as 20 (Rabor, 1977, p. 238), 20–24 (Rabor, 1955, p. 211), and 50 or more (FMNH 56161–56162, field notes). One solitary old male has been observed (Hoogstraal, 1951, p. 45). No information is available concerning the size of home ranges.

Little is known concerning breeding in natural populations of Philippine *M. fascicularis.* In a captive colony maintained outdoors at Tanay, in southern Luzon near Manila, the frequency of births peaks strongly in May (table 11), which is near the beginning of the rainy season (Ulack & Pauer, 1989, p. 64); during 1985–1987 more than three times as many infants were born in May as were born in January or February, at the beginning of the dry season. Concordantly, fetuses in two wild-collected pregnant females (USNM 144683, 144684) obtained 1 March 1907 at Nagpartian, northern Luzon, probably would have been born near the beginning of the rainy season. The month-

TABLE 8. Local variation of accessory entostyle frequency in M^2 and M^3 in Mindanao *M. fascicularis*.

Sample areas[1]	Approximate center of sample area		Number of teeth	Entostyle frequency
	N lat.	E long.		
Zamboanga; San Ramon (*117, 118*)	7°00′	122°00′	8	0.12
Katipunan Munic. (*110–112*)	8°30′	123°15′	74	0.41
Mt. Malindang area; Bucong (*107–109, 113*)	8°00′	123°30′	76	0.39
Pantar; Lake Lanao (*105, 106*)	8°00′	124°15′	32	0.69
Bugusan; Burungkot; Maculi Pt. (*101–103*)	6°45′	124°15′	14	0.50
Mt. Apo area; Caburan; Kamansi (*91, 94, 95, 97, 99*)	7°00′	125°15′	38	0.42

[1] Listed in west–east order. Locality numbers in parentheses (see fig. 1).

ly distribution of births in the Tanay colony of *M. fascicularis* generally resembles that in *M. fascicularis* in West Malaysia, where births peak in June (Kavanagh & Laursen, 1984, p. 23; reference provided by anonymous reviewer). The birth peak in May in the Tanay colony also is close to the mid-June birth season of the fruit bat *Haplonycteris fischeri* studied in northern Luzon, southern Negros, and southern Bohol by Heideman (1988, p. 586); in fruit bat populations studied in Biliran and central Leyte, the birth season occurs later, in July or August. Copulations in the Tanay colony peak during the period October–March (R. G. Resuello, SICONBREC, pers. comm., 4 Aug. 1989), which accords with the 5.5-month gestation period in *M. fascicularis* (Ardito, 1976, p. 216). In 1987, the annual reproductive rate in the Tanay colony was 0.76 surviving weaned young per breeding female (Hobbs, 1989, p. 64).

In nature, females enter the breeding population

TABLE 9. Blood-protein allele frequencies at polymorphic loci in Philippine and non-Philippine *M. fascicularis*. For references and details, see Fooden and Lanyon (1989, pp. 216, 222).

Locus	Abbreviation	Allele	Allele frequencies (%) and sample sizes (in parentheses)			
			Philippines: Mindanao	Philippines: island unknown	Sumatra[1]	Other *M. fascicularis*[1]
Albumin, plasma	Alb	A	100 (58)	100 (21)	89 (222)	98 (734)
Carbonic anhydrase-II, cell	CA-II	A	62 (16)	...	...	59 (133)[2]
		B	38			41
Hemoglobin-alpha, cell	HbA	1	50 (59)	50 (21)	58 (222)	72 (1,077)
		2	50	50	42	24
Isocitrate dehydrogenase, cell	IDH	1	...	98 (21)	89 (222)	58 (516)
		2		2	10	42
6-phosphogluconate dehydrogenase, cell	PGD	A	100 (78)	100 (21)	89 (218)	95 (912)
Phosphoglucomutase-I, cell	PGM-I	1	...	90 (21)	98 (221)	96 (481)
		4		10	0	3
Phosphohexose isomerase, cell	PHI	1	57 (30)	81 (21)	99 (223)	99 (648)
		2	0	2	0	0
		5	43	17	1	< 1
Protease inhibitor, plasma	PI	A	2 (54)	0 (73)	1 (291)	1 (1,034)
		B	93	96	80	60
		C	5	4	19	38
Thyroxine-binding prealbumin, plasma	TBPA	F	94 (58)	96 (73)	90 (274)	90 (108)
		S	6	4	10	10
Transferring, plasma	Tf	D	100 (78)	100 (73)	59 (244)	50 (913)

[1] Table excludes minor alleles present in non-Philippine *M. fascicularis* but absent in Philippine *M. fascicularis*.
[2] Includes unlocalized sample (N = 67; 0.75 A, 0.25 B) inadvertently omitted from data table in Fooden and Lanyon (1989, table IV).

TABLE 10. Habitat observations of Philippine *M. fascicularis*.

Observer	Year	Island	Reference
		Seashore	
J. B. Steere	1874	Basilan, Luzon, Mindanao, Palawan	Günther, [1877], p. 735
P. C. Frier et al.	1906	Palawan	Mearns MS. (USNM)
E. A. Mearns	1906	Tawitawi	Mearns MS. (USNM)
		Sand Ridges	
E. A. Mearns	1907	Luzon	Mearns MS. (USNM)
		Swamp Forest	
E. A. Mearns	1903	Jolo	Mearns MS. (USNM)
E. A. Mearns	1904	Cagayan Sulu	Mearns MS. (USNM)
		Riverine Forest	
E. A. Mearns	1906	Samar	Mearns MS. (USNM)
H. Hoogstraal et al.	1946	Luzon	FMNH 62273–62274, notes
D. S. Rabor and F. Werner	1947	Palawan	FMNH 62901, note
		Cultivated Field	
E. A. Mearns	1906	Basilan	Mearns MS. (USNM)
H. Hoogstraal	1947	Mindanao	FMNH 56995, note
E. A. Rickart et al.	1987	Maripipi	Rickart et al., in prep.
Mr. Siloy	1987	Leyte	L. R. Heaney (FMNH), field notes
		Open Grassland	
E. A. Mearns	1904	Mindanao	Mearns MS. (USNM)
		Second-Growth Forest	
P. Añonuevo	1947	Culion	PNM 1196, note
D. S. Rabor	1947	Culion	FMNH 62908, note
D. S. Rabor	1947	Palawan	FMNH 62914, note
H. T. Wright et al.	1947	Palawan	FMNH 62905, 62913, notes
		Primary Rain Forest, Edge	
E. A. Rickart et al.	1987	Biliran	Rickart et al., in prep.
		Primary Rain Forest	
E. v. Martens	1861	Luzon, Mindanao	Martens, 1876, p. 193
E. A. Mearns	1903	Mindanao	USNM 123450, note
M. Celestino	1946	Mindanao, 3 localities	FMNH 56435–56437, notes
H. Hoogstraal et al.	1946	Luzon	FMNH 62275–62276, notes
D. S. Rabor	1947	Busuanga	FMNH 62906, note
H. Hoogstraal	1947	Mindanao	FMNH 56495, note
L. R. Heaney	1984	Leyte	UMMZ 161311, note (pers. comm., 14 Mar. 1990)
E. A. Rickart et al.	1987	Maripipi	Rickart et al., in prep.
		Montane Forest (850 m)	
E. A. Rickart et al.	1987	Biliran	Rickart et al., in prep.
		Mossy Forest (2000 m)	
H. Hoogstraal	1946	Mindanao	Hoogstraal, 1951, p. 44
		Oak-pine Montane Forest (2300 m)	
J. Whitehead	1895	Luzon	Thomas, 1898, p. 381

before they achieve dental maturity. A wild-collected female (USNM 477849, Apr. 1962, field note) with third molars unerupted (age < 4.5 years; Hurme, 1960, p. 797; Bowen & Koch, 1970, p. 122) was already pregnant, and another (USNM 144675, Nov. 1906, field note) with third molars erupting (age ca. 6 years) evidently had already nursed an infant.

TABLE 11. Monthly distribution of births in captive colony of Philippine *M. fascicularis* maintained outdoors at Tanay, near Manila (Hobbs, 1989, p. 67).

	1985		1986		1987[1]		Total[1]	
Month	N	%	N	%	N	%	N	%
Jan.	2	0.6	30	5.7	56	5.8	88	5.0
Feb.	6	1.8	26	4.9	52	5.4	84	4.8
Mar.	28	8.2	54	10.3	62	6.4	144	8.2
Apr.	26	7.6	62	11.8	116	12.0	204	11.6
May	60	17.6	88	16.7	154	15.9	302	17.1
June	41	12.0	72	13.7	138	14.3	251	14.2
July	42	12.3	74	14.0	116	12.0	232	13.2
Aug.	28	8.2	36	6.8	75	7.8	139	7.9
Sep.	54	15.9	18	3.4	100	10.4	172	9.7
Oct.	32	9.4	17	3.2	97	10.0	146	8.3
Nov.	12	3.5	22	4.2	nd[2]	...	...	...
Dec.	10	2.9	28	5.3	nd[2]	...	...	...
TOTALS	341	100.0	527	100.0	966	100.0	1,762	100.0

[1] Ten-month period.
[2] No data.

Systematics

Subspecific Taxonomy

Geographic variation within or between Philippine *M. fascicularis* and Sabah *M. fascicularis* is apparent in (1) dorsal pelage color, (2) head and body length, (3) relative tail length, (4) greatest skull length, and (5) incidence of accessory entostyles (see above). Of these, dorsal pelage color traditionally has served as the primary basis for recognition of subspecies in *M. fascicularis* and, as discussed below, continues to provide the most useful criterion for subspecific allocation of Philippine and Sabah populations of this species.

Head and body length and greatest skull length average greater in Philippine *M. fascicularis* than in Sabah *M. fascicularis,* and, conversely, relative tail length averages greater in Sabah *M. fascicularis* than in Philippine *M. fascicularis* (tables 3, 5). However, overlap between Philippine and Sabah samples is substantial in all three of these characters. Greatest skull length varies clinally within Philippine *M. fascicularis* and probably also between Philippine *M. fascicularis* and Sabah *M. fascicularis* (fig. 7). Similar clinal variation within and between Philippine and Sabah *M. fascicularis* also may occur in head and body length and relative tail length.

The incidence of accessory entostyles is geographically erratic in Philippine and Sabah *M. fascicularis* (table 7). The incidence of entostyles is relatively high in Sabah, Mindanao, and Mindoro and generally is low elsewhere in the Philippines.

Dorsal pelage color in *M. fascicularis* is distinctively dark in most islands of the Philippine archipelago (fig. 3). The major known exceptions are the south-central islands of Cagayan Sulu, Tawitawi, Basilan, and western Mindanao. In these islands, dorsal pelage color is pale to intermediate, matching in saturation that in nearby Sabah *M. fascicularis.* In central and southeastern Mindanao and in southern Negros, dorsal pelage color varies from pale to intermediate to dark.

Variation of dorsal pelage color in Philippine *M. fascicularis* is at least partly independent of variation of skull length; in southern Philippine samples, skull length is small but pelage color may be either pale or dark (figs. 3, 7). Similarly, variation of pelage color also is partly independent of variation of incidence of accessory entostyles; pelage color is pale in Sabah and dark in Mindoro, but entostyle incidence is relatively high in both of these places (table 7). Variation of pelage color probably also is at least partly independent of variation of head and body length and relative tail length.

Taxonomically, pale to intermediate populations of *M. fascicularis* in south-central Philippines are referable to the same subspecies as those in neighboring Sabah (fig. 9); assuming that these pale populations are inseparable from those in southern Sumatra, the name that applies to this pale subspecies is *M. fascicularis fascicularis* Raf-

fles, [1821] (type locality, Bengkulu vicinity, southern Sumatra). Dark populations of Philippine *M. fascicularis* that are geographically contiguous constitute another subspecies, for which the name *M. fascicularis philippinensis* I. Geoffroy, [1843] (type locality, "Manile"), is available. The area of mixed populations of pale, intermediate, and dark individuals in central and southeastern Mindanao and southern Negros is geographically intermediate between the subspecific ranges of *M. f. philippinensis* and *M. f. fascicularis* as defined above and may be regarded as a subspecific contact zone. The current taxonomic practice (cf. Napier, 1981, p. 13) of uniting pale and dark populations of Philippine *M. fascicularis* in a single taxon that excludes pale Sabah *M. fascicularis* is untenable.

For most nonvolant mammals, the faunal relationship between Borneo and Palawan is closer than that between Borneo and Mindanao (Heaney, 1986, p. 141). The reverse is true for subspecies of *M. fascicularis* (fig. 9).

A single specimen collected in Busuanga Island, in the Palawan–Mindoro chain, and another collected in Balut Island, south of Mindanao, are problematical (fig. 3). The Busuanga specimen is intermediate in dorsal pelage color saturation and may be assigned either to *M. fascicularis* or to the contact-zone area; both of these assignments are geographically incongruous. The Balut specimen is dark, which implies either that this island is part of the subspecific contact zone or that it is a disjunct extension of the range of *M. f. philippinensis.*

Subspecies Accounts

Macaca fascicularis fascicularis

(Raffles, [1821], p. 246), part, Philippine Islands only

Macacus philippensis: Murray, 1885, p. 665 (not Reichenbach, 1862)—Mindanao: Mount Pulunbato.

Macacus philippinensis: Steere, 1890, p. 28 (part, not I. Geoffroy, [1843])—Basilan. Bourns and Worcester, 1894, p. 61—Basilan, Jolo, Tawitawi.

Cynomolgus suluensis Mearns, 1905, p. 430—holotype, USNM 125324, adult male, skull only, collected 16 Nov. 1903 by E. A. Mearns, Jolo: foot of Crater Lake Mountain. Hill, 1974, p. 522—a synonym of *Macaca irus philippinensis.*

Macaca suluensis: Lyon and Osgood, 1909, p. 284—holotype cataloged.

M[acaca] p[hilippinensis] suluensis: Rabor, 1986, p. 138—distribution, Sulu archipelago.

Pithecus sulensis: Hollister, 1912, p. 37—listed. Elliot, [1913], p. 252—specific status indeterminate.

Macaca suluana: Alcasid, [1970], p. 24—listed.

Macaca sulvensis: Chiarelli, 1972, p. 213—species name incorrectly spelled.

Cynomolgus cagayanus Mearns, 1905, p. 431—holotype, USNM 125325, adult male, skin and skull, collected 25 Feb. 1904 by E. A. Mearns, Cagayan Sulu. Napier, 1981, p. 13—a synonym of *Macaca fascicularis philippinensis.*

Macaca cagayana: Lyon and Osgood, 1909, p. 283—holotype cataloged.

Macaca irus cagayana: Hill, 1974, p. 525—external and cranial characters ex Mearns, 1905.

M[acaca] p[hilippinensis] cagayanus: Rabor, 1986, p. 138—distribution, Cagayan Sulu.

Pithecus cagayanus: Hollister, 1912, p. 36—listed.

TYPE—None preserved. The name *Simia fascicularis* Raffles, [1821], is based on specimens collected between 1818 and 1820 in Sumatra by T. S. Raffles. Three syntypes formerly were preserved in the collection of the Zoological Society of London (Waterhouse, 1838, p. 7).

TYPE LOCALITY—Indonesia: Sumatra, near Bengkulu (Hill, 1974, p. 477).

DISTRIBUTION—The known range of Philippine *Macaca f. fascicularis* is restricted to the south-central part of the Philippine archipelago, including Cagayan Sulu, the Sulu archipelago (Tawitawi, Basilan), and western Mindanao (west of 123°30′E) (figs. 3, 9). A single specimen with golden brown agouti pelage also has been collected in Busuanga, which is disjunct from the range given above; the zoogeographic significance of this specimen is unclear (see above, Subspecific Taxonomy).

DIAGNOSIS—Dorsal pelage color in Philippine *M. f. fascicularis* is pale yellowish brown agouti (olivaceous) to golden brown agouti and is variably erythristic. Pelage color in Philippine *M. f. fascicularis* is similar in saturation to that in Sabah *M. f. fascicularis,* but averages somewhat more erythristic.

Macaca fascicularis philippinensis

I. Geoffroy, [1843]

Macacus cynomolgus: Waterhouse, 1838, p. 8—part, specimen collected in Luzon. Cuming, [1841], p. 33—color variation. Gray, 1849, p. 4—part, Philippines included in geographic range. Thomas, 1898, p. 381—Luzon: Barit.

C[ynamolgus] cynamolgus: Elera, 1895, p. 2—part, Philippines included in geographic range. Elera, 1915, p. 32—part, dorsal pelage color.

Macacus carbonarius: Waterhouse, 1839, p. 2—part, revised identification of *Macacus cynomolgus*: Waterhouse, 1838.

Macacus philippinensis I. Geoffroy, [1843], p. 568, pl. 5 (animal)—name based on captive albino, proposed provisionally. I. Geoffroy, 1851, p. 29—type history. Gervais, 1854, p. 88—behavior of holotype in captivity. Schlegel, 1876, p. 104—a synonym of *Cercocebus cynamolgus.*

Macacus philippensis: Anderson, 1879, p. 74—species name incorrectly spelled.

Macaca philippinensis: Kellogg, 1945, p. 119—listed.

Macaca philippensis: Kuntz, 1969, p. 217—species name incorrectly spelled.

Macaca phylippinensis: Chiarelli, 1972, p. 213—species name incorrectly spelled.

Pith[ecus] (Mac[acus]) Philippinensis: Dahlbom, 1856, p. 118—external characters.

C[ynamolgus] philippensis: Reichenbach, 1862, p. 134—species name incorrectly spelled.

C[ynamolgus] philippinensis: Elera, 1895, p. 2—listed.

Cynomolgus philippinensis: Mearns, 1905, p. 426—external and cranial characters.

Zati philippensis: Reichenbach, 1862, p. 135—preferred binomial.

Cercocebus Philippinus: Martens, 1876, p. 207—species name incorrectly spelled.

[*Silenus*] *philippinensis:* Stiles and Nolan, 1929, p. 532—new generic combination.

Macacus cynamolgos . . . var. *Philippinus:* Martens, 1876, pp. 193, 362—Luzon: Los Baños.

Macaca philippinensis philippinensis: Sanborn, 1952, p. 113—taxonomic comparison.

Macaca irus philippinensis: Hill, 1974, p. 522—taxonomy.

[*Macaca fascicularis*] *philippinensis:* Napier and Napier, 1967, p. 404—listed.

Macacus palpebrosus I. Geoffroy, 1851, pp. 88, 93—syntypes, four captives presented by M. Dugast to menagerie of MNHN about 1851, obtained in Luzon: "forêts de Manille," apparently not preserved (cf. Rode, 1938, p. 222); name proposed provisionally. I. Geoffroy, [1852], p. 543—type history. Schlegel, 1876, p. 104—a synonym of *Cercocebus cynamolgos.* Martens, 1876, p. 206—a synonym of *Macacus cynamolgos* var. *Philippinus.* Mearns, 1905, p. 426—a synonym of *Cynomolgus philippinensis.*

I[nuus] palpebrosus: Wagner, 1855, p. 54—specific status questionable.

C[ynamolgus] palpebrosus: Reichenbach, 1862, p. 137—external characters ex I. Geoffroy, 1851.

Macacus fur Slack, 1867, p. 36, pl. 1 (animal; skull)—holotype, formerly preserved in Academy of Natural Sciences, Philadelphia (ANSP), no. 1254, adult male, skin and skull, obtained "some years since" in Paris by J. H. Slack (1867), said to inhabit Luzon; holotype now lost (J. E. Cadle, ANSP, letter, 14 Nov. 1989; cf. Koopman, 1976, p. 7). Schlegel, 1876, p. 104—a synonym of *Cercocebus cynamolgos.* Hollister, 1912, p. 37—a synonym of *Pithecus syrichta.*

C[ynamolgus] fur: Elera, 1895, p. 3—listed.

Macacus cynomolgus . . . var. *Cumingii* Gray, 1870, p. 30—holotype, BM(NH) 1859.7.9.5, juvenile female, skin and skull, obtained (presumably in 1859) from J. Verreaux, "*Hab.* Philippine Islands." Schlegel, 1876, p. 104—allocated to Philippine "conspecies." Hollister, 1912, p. 37—a synonym of *Pithecus syrichta.*

C[ynamolgus] var. cumingii: Elera, 1895, p. 3—listed.

[*Cynomolgus*] *fascicularis:* Trouessart, 1904, p. 16—part, Philippines included in geographic range.

Macacus fascicularis: Elliot, 1907, p. 567—Panay.

M[acaca] syrichta: Thomas, 1911, p. 129 (not Linnaeus, 1758)—misidentification of holotype of *Simia syrichta* Linnaeus, 1758, p. 29 (a tarsier; cf. Cabrera, 1923, p. 90). Elliot, [1913], p. 249—a synonym of *Pithecus philippinensis.*

Pithecus syrichta: Hollister, 1912, p. 37 (not Linnaeus, 1758)—distribution: Luzon, Leyte, Mindoro, Negros, Palawan, Samar. Hollister, 1913, pp. 328, 330—invalid designation of neotype.

S[ilenus] syrichta: Stiles and Nolan, 1929, p. 537 (not Linnaeus, 1758)—nomenclature.

Pithecus mindorus Hollister, 1913, p. 328, pls. 27–28 (skull)—holotype, USNM 144674, adult male, skin and skull, collected 1–8 Nov. 1906 by E. A. Mearns, Mindoro: Alag River. Hill, 1974, p. 522—a synonym of *Macaca irus philippinensis.*

Macaca mindorus: Poole and Schantz, 1942, p. 244—holotype cataloged.

M[acaca] p[hilippinensis] mindorus: Rabor, 1986, p. 138—distribution, Mindoro.

Macaca mindora: Lawrence, 1939, p. 63—taxonomic comparison.

[*Macaca fascicularis*] *mindora:* Napier and Napier, 1967, p. 404—listed.

Macaca irus: Pocock, 1939, p. 78—part, Philippine Islands included in distribution.

TYPE—The holotype of *Macacus philippinensis* I. Geoffroy, [1843], is MNHN 373/265, albino adult male, mounted skin only (omitted from type catalog published by Rode, 1938, p. 222). This monkey was obtained alive in Manila by A. Chenest and presented by him to the menagerie of MNHN on 6 Aug. 1841; it died on 29 Aug. 1842 (cf. I. Geoffroy, 1851, p. 29).

TYPE LOCALITY—Philippine Islands: probably Luzon. Concerning the provenance of the holotype, I. Geoffroy [1843, p. 570] reports: "M. Adolphe Chenest, qui a fait don au Muséum de Singe précieux, l'a acquis à Manille, et il le croit originaire de cette île."

DISTRIBUTION—The known range of *M. f. philippinensis* includes Balabac, Palawan, Culion, Mindoro, Luzon, Samar, Leyte, and northeastern Mindanao (north of ca. 9°00′N) (figs. 3, 9). The subspecific range probably also includes other islands in central Philippines, north of ca. 10°00′N lat. A single specimen with dark dorsal pelage was collected in Balut, south of Mindanao; the zoogeographic significance of this specimen is ambiguous (see above, Subspecific Taxonomy).

DIAGNOSIS—Dorsal pelage color in *M. f. philippinensis* is dark brown agouti, variably erythristic.

TAXONOMIC NOTE—*Macacus cristatus* Gray, 1870 (p. 30) has been treated as a synonym of *Macacus philippinensis* I. Geoffroy, [1843], by Elliot ([1913], p. 249) and subsequent authors. However, this name may not be based on a Philippine macaque. The holotype of *Macacus cristatus* is BM(NH) 1858.4.28.9, an albinistic late juvenile male, skin and skull, obtained in 1858 from the collection of Th. G. van Lidth de Jeude, Utrecht (cf. Thomas, 1906, p. 43; Napier, 1981, p. 20). No information was available to Gray concerning the provenance of the specimen ("*Hab.* ____?"). In Gray's description of *cristatus,* he compares external characters of the albinistic holotype with those of the albino holotype of *Macacus philippinensis* I. Geoffroy; this may be the source of Elliot's assumption that the holotype of *cristatus* originated in the Philippines (cf. Anderson, 1879, p. 76). Independent retrospective inquiry into the geographic origin and subspecific identity of the holotype of *cristatus* is impeded by the immaturity and deficient pigmentation of the specimen.

Macaca fascicularis fascicularis/
Macaca fascicularis philippinensis
Contact Zone

Macaca philippinensis: Steere, 1890, p. 28 (part, not I. Geoffroy, [1843])—Mindanao, Negros.

Cynomolgus mindanensis Mearns, 1905, p. 428—holotype, USNM 123450, adult male, skin and skull, collected 26 Aug. 1903 by E. A. Mearns, Mindanao: Pantar. Elliot, [1913], p. 250—a synonym of *Pithecus philippinensis.* Hill, 1974, p. 522—a synonym of *Macaca irus philippinensis.*

Macaca mindanensis: Lyon and Osgood, 1909, p. 284—holotype cataloged.

Pithecus mindanensis: Hollister, 1913, p. 329—taxonomy.

Pithecus mindanensis mindanensis: Hollister, 1912, p. 37—listed.

Macaca philippinensis mindanensis: Sanborn, 1952, p. 113—taxonomic comparison. Rabor, 1986, p. 138—distribution, Panay, Samar, Leyte, Bohol, Cebu, Negros, Mindanao, Basilan.

[*Macaca fascicularis*] *mindanensis:* Napier and Napier, 1967, p. 404—listed.

Cynomolgus mindanensis apoensis Mearns, 1905, p. 429—holotype, USNM 125321, adult female, skin and skull, collected 25 June 1904 by E. A. Mearns, Mindanao: Mount Apo. Hollister, 1913, p. 329—subspecies regarded as unrecognizable.

Macaca mindanensis apoensis: Lyon and Osgood, 1909, p. 283—holotype cataloged.

Pithecus mindanensis apoensis: Hollister, 1912, p. 37—listed.

Pithecus philippinensis apoensis: Elliot, [1913], p. 250—subspecies recognized provisionally.

DISTRIBUTION—Mixed populations that include individuals with pale, intermediate, and dark dorsal pelage are documented in southern Negros (south of 9°40′N) and in central and southeastern Mindanao (south of 8°10′N, east of 123°40′E) (figs. 3, 9).

DIAGNOSIS—Dorsal pelage color in the *M. f. fascicularis/M. f. philippinensis* contact zone varies from pale yellowish brown agouti to golden brown agouti to dark brown agouti and is variably erythristic.

Zoogeography and Evolution

The Philippine archipelago is separated from Borneo and other islands on the Sunda Shelf by deep trenches (minimum depth 145 m, Balabac–Palawan chain; 290 m, Sulu archipelago; Heaney, 1985b, p. 54). Most Philippine nonvolant mammals probably dispersed to the archipelago from Borneo during periods of Pleistocene continental glaciation when worldwide sea-level regression reduced the width of intervening water gaps (Heaney, 1986, p. 152; Van Couvering & Kukla, 1988b, p. 507). During the most recent glacial maximum (ca. 18,000 years B.P.), sea level was about 120 m lower than at present; during the immediately preceding glacial maximum (ca. 160,000 years B.P.), sea level was about 160 m lower than at present (Heaney, 1985a, p. 129; Van Couvering & Kukla, 1988a, p. 462).

The most conspicuous zoogeographic pattern in Philippine *M. fascicularis* is the restricted distribution of pale to intermediate *M. f. fascicularis* in south-central islands (Cagayan Sulu, Sulu archipelago, western Mindanao), the relatively broad distribution of dark *M. f. philippinensis* in western, northern, and eastern islands (Balabac, Palawan, Culion, Mindoro, Luzon, Samar, Leyte, northeastern Mindanao, and presumably others), and the intervening distribution of pale to intermediate to dark contact-zone populations (eastern and southern Mindanao, southern Negros) (figs. 3, 9). Pale to intermediate *M. f. fascicularis* also inhabits Sabah. Either of two alternative hypotheses can account for this pattern. A "one-wave" hypothesis postulates that *M. fascicularis* dispersed from Borneo to the Philippines once, becoming progres-

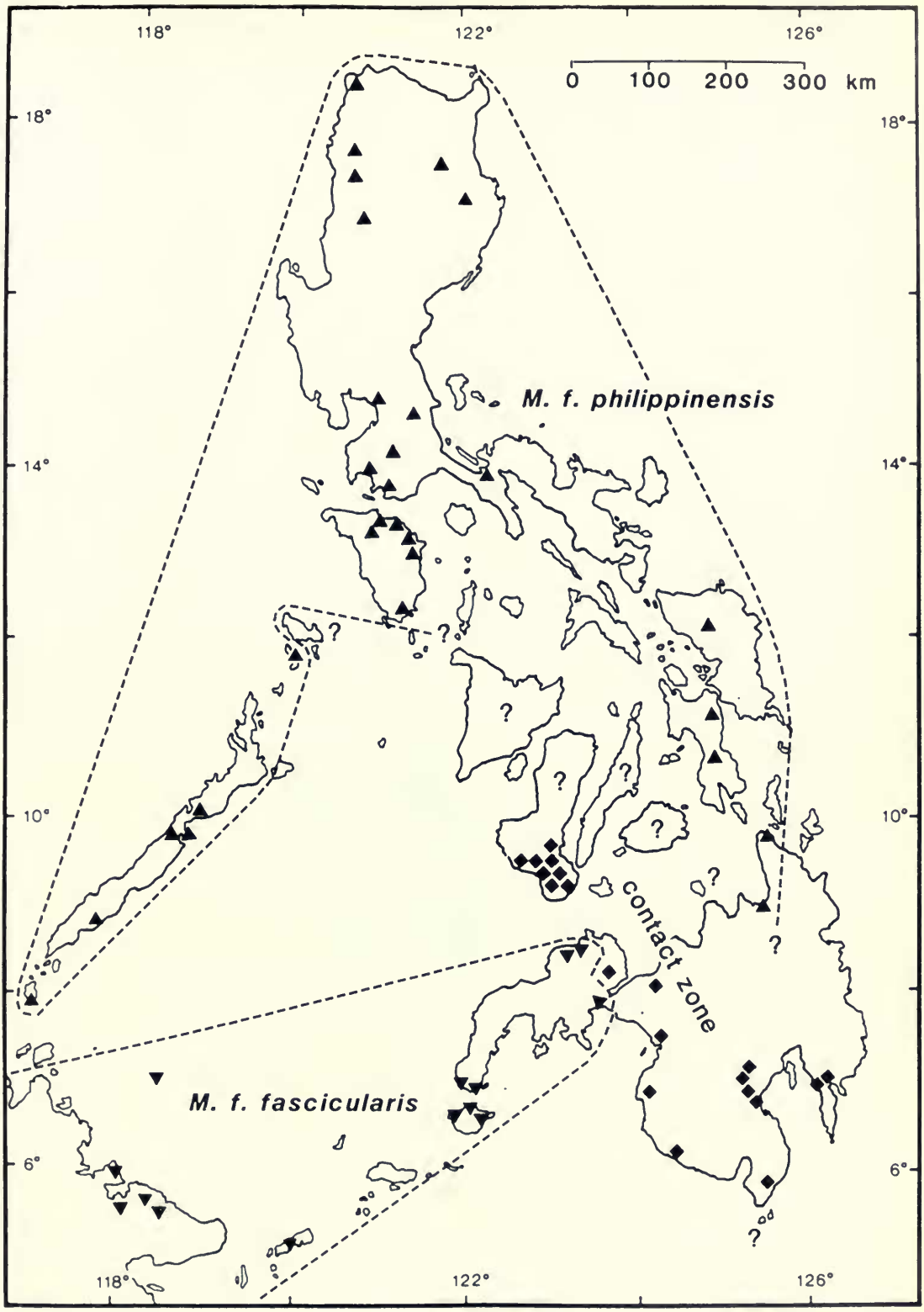

FIG. 9. Known limits of distribution of Philippine *M. f. fascicularis, M. f. philippinensis,* and contact-zone populations (cf. fig. 3).

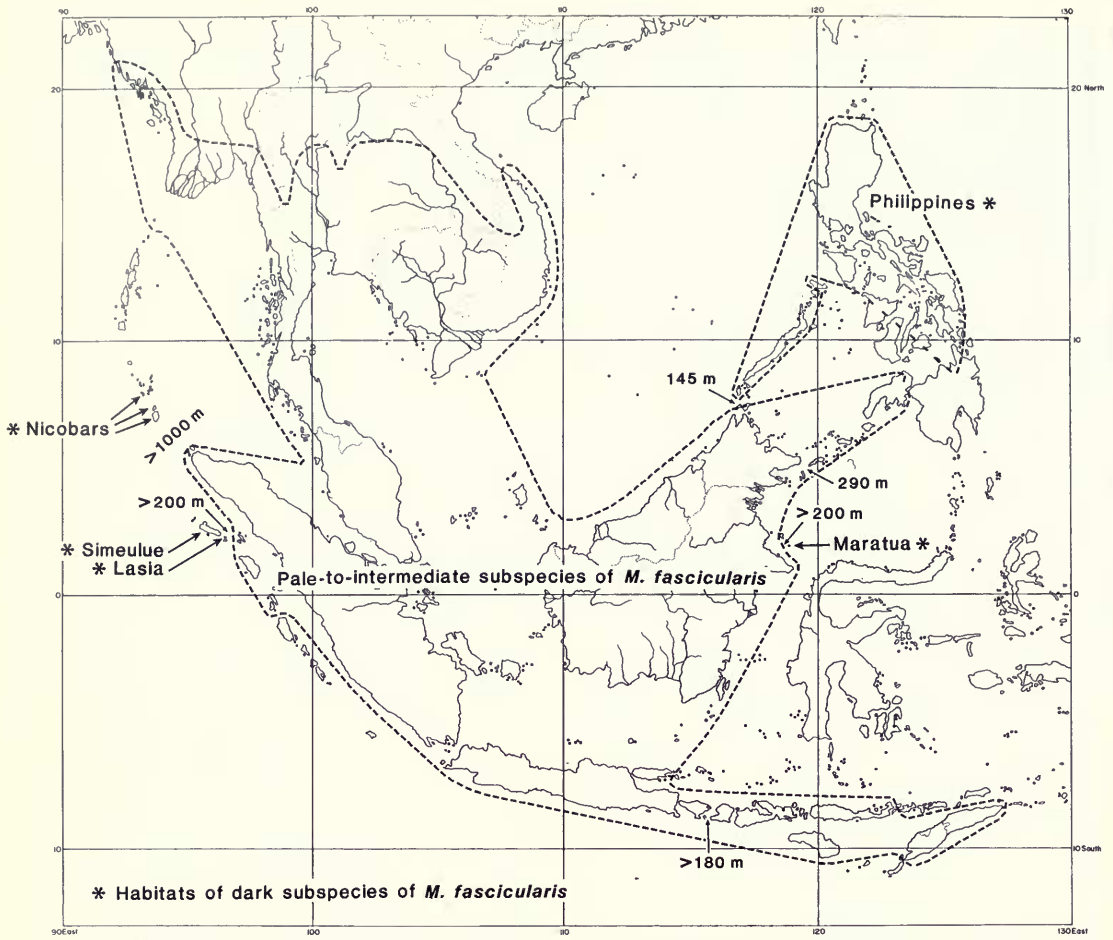

FIG. 10. Map of Southeast Asia showing limits of distribution of pale to intermediate subspecies of *M. fascicularis,* location of deep-water insular habitats of dark subspecies of *M. fascicularis,* and depth of intervening channels. (References: Chasen, 1940, p. 68; Kellogg, 1944, p. 76; Defense Mapping Agency Hydrographic Center, 1973, 1975, 1979; Fooden, 1980, p. 5; Heaney, 1985b, p. 54; Khan, 1985, p. 29; above, figs. 3, 9.)

sively darker as it spread through the archipelago, thus producing the present pattern of color variation. A "two-wave" hypothesis, discussed in greater detail below, postulates that *M. fascicularis* dispersed to the Philippines twice, with the first wave now represented by dark *M. f. philippinensis* and the second wave now represented by pale to intermediate *M. f. fascicularis.* The species-wide geographic distribution of pale to intermediate and dark populations of *M. fascicularis* tends to favor the two-wave hypothesis.

Outside of the Philippines, pale to intermediate populations of *M. fascicularis* are broadly distributed, from southernmost Bangladesh, through the Indochinese and Malay peninsulas, Sumatra, Java, Borneo, and numerous adjacent smaller islands, to Timor in the Lesser Sunda Islands (fig. 10; Chasen, 1940, p. 68; Kellogg, 1944, p. 76). Non-Philippine dark populations of *M. fascicularis* are restricted to three island groups or islands around the periphery of the specific range: (1) Nicobar Islands, NW of Sumatra; (2) Pulau Simeulue and Pulau Lasia, W of Sumatra; and (3) Pulau Maratua, E of Borneo (fig. 11). Most islands inhabited by pale to intermediate populations of *M. fascicularis* are shallow-water islands on the Sunda Shelf; the only deep-water islands inhabited by pale to intermediate *M. fascicularis* are the south-central Philippine Islands and the Lesser Sunda Islands. By contrast, all four island groups or islands that are inhabited by dark populations of *M. fascicularis,* including *M. f. philippinensis,* are deep-water islands, separated from the Sunda Shelf by deep trenches (Nicobar Islands, > 1000 m; Pulau Si-

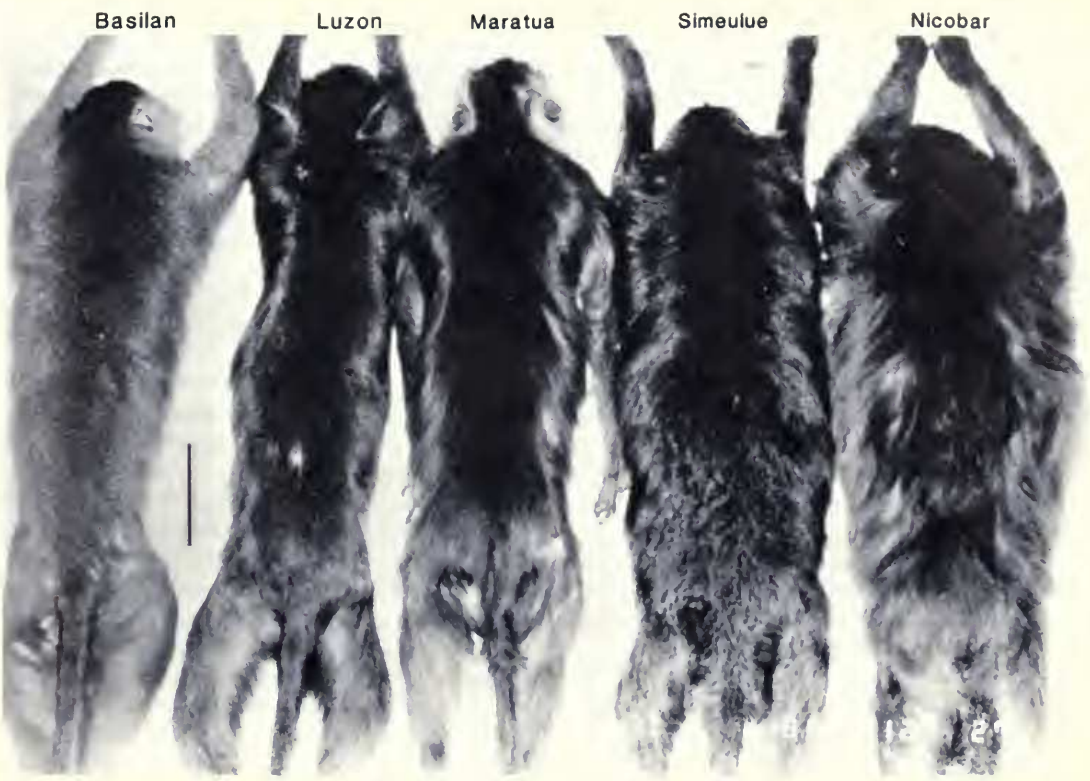

FIG. 11. Dark non-Philippine *M. fascicularis* skins (USNM 197662, Pulau Maratua; USNM 114168, Pulau Simeulue; USNM 111797, Little Nicobar I.) compared with pale and dark Philippine *M. fascicularis* skins (USNM 144666, Basilan: E end; USNM 144676, Luzon: Nagpartian). Scale bar 10 cm.

meulue and Pulau Lasia, > 200 m; Pulau Maratua, > 200 m).

Dorsal pelage is pale to intermediate not only in most populations of *M. fascicularis* but also in *Macaca mulatta,* a close relative of *M. fascicularis* (Fooden, 1980, p. 7). This suggests that pale to intermediate pelage is primitive in *M. fascicularis* and that dark pelage evolved independently in the four deep-water island populations, which presumably have been isolated longer than pale to intermediate shallow-water island populations. These pale to intermediate shallow-water island populations of *M. fascicularis* probably were geographically and genetically continuous during the most recent glacial maximum (ca. 18,000 years B.P.), and they probably have been isolated only since the subsequent postglacial rise of sea level. *Macaca f. philippinensis* and the other three dark populations may have dispersed to their deep-water island habitats during the preceding glacial maximum (ca. 160,000 years B.P.) and may have been isolated since the corresponding interglacial rise of sea level. Complete land bridges to the deep-water islands would not have been required for *M. fascicularis* to reach them; this species swims well and often forages along the seashore, and therefore was a prime candidate for active or passive overwater dispersal when the penultimate glacial sea-level depression (ca. 160 m) greatly narrowed the water gaps that separate deep-water islands from the Sunda Shelf.

To recapitulate, the first wave of *M. fascicularis* is assumed to have reached the Philippines from Borneo during the penultimate glacial maximum; in isolation, during the subsequent interglacial, this population differentiated into dark *M. f. philippinensis.* The second wave of *M. fascicularis* reached the Philippines from Borneo during the most recent glacial maximum; during its much shorter period of postglacial isolation, this population has retained the pale to intermediate pelage of *M. f. fascicularis.* (The dispersal of *M. fascicularis* to the Lesser Sunda Islands may also have occurred during the most recent glacial maximum; this is suggested by the pale to intermediate pelage of Lesser Sunda populations.) The dispersal route

of the first wave may have been either by way of the Balabac–Palawan chain or by way of the Sulu archipelago, or by both. The dispersal route of the second wave evidently was by way of the Sulu archipelago. The slow loris, *Nycticebus coucang,* with one subspecies inhabiting both Borneo and the Sulu archipelago (Groves, 1971, p. 49; Musser & Heaney, 1985, p. 29), provides additional evidence of a relatively recent dispersal route for primates from Borneo via the Sulu archipelago. Cagayan Sulu, the Sulu archipelago, and western Mindanao formerly may have been inhabited by dark first-wave populations of *M. f. philippinensis* that were displaced by pale to intermediate second-wave populations of *M. f. fascicularis.* The *M. f. fascicularis/M. f. philippinensis* contact zone in central and southeastern Mindanao and southern Negros may be the result of interbreeding between dark first-wave populations and pale to intermediate second-wave populations. A dark specimen collected in Balut Island, off southern Mindanao (fig. 3), may represent a population that is a geographic relict of the first wave.

After becoming isolated in the Philippines, in addition to undergoing darkening of dorsal pelage, *M. fascicularis* also apparently increased in size—at least cranially—as it dispersed northward; this is a frequent pattern of geographic variation in macaque species (cf. Fooden, 1988, p. 8). The incidence of accessory entostyles apparently has decreased independently in several islands following isolation of populations of *M. fascicularis*; the high frequency of entostyles that presumably characterized the ancestral population in Borneo apparently has been retained in Mindanao and Mindoro (possibly also in Panay, Balut, and Basilan). Blood-protein loci apparently have tended to become fixed in isolated populations of Philippine *M. fascicularis*; additional localized blood-protein data from Bornean and Philippine *M. fascicularis* would provide a critical test of the two-wave hypothesis. In the absence of other species of macaques, Philippine *M. fascicularis* apparently has successfully expanded its ecological range to include primary evergreen rain forest ("ecological release"). Proliferation of *M. fascicularis* in the Philippines may have been a factor in the origin and evolution of the endemic Philippine eagle *Pithecophaga jefferyi,* a known predator on these monkeys.

Transport by humans of pet monkeys is frequently assumed to have been a major factor in the dispersal of *M. fascicularis* to and within the Philippine archipelago (Blyth, 1875, p. 8; Whitehead in Thomas, 1898, p. 381; Taylor, 1934, p. 340; Darlington, 1957, p. 504). No data are available on which to base an estimate of the impact of human introductions on the distribution of Philippine macaques. However, as indicated above, the habits of this species are conducive to natural overwater dispersal. In any event, it seems highly unlikely that the broad coherent pattern of distribution in the archipelago of *M. f. fascicularis, M. f. philippinensis,* and contact-zone populations is essentially an artifact produced by the random transport of pets.

Summary

Dorsal pelage color in Philippine *M. fascicularis* is pale to intermediate in south-central islands of the archipelago—as in Sabah, northern Borneo—and dark in most other islands; in central and southeastern Mindanao and in southern Negros, dorsal pelage color varies from pale to intermediate to dark. Available external measurements are inadequate to establish a pattern of geographic variation of size; greatest skull length, however, increases latitudinally from Sabah to Luzon. Blood-protein loci tend to be less variable in Philippine *M. fascicularis* than in non-Philippine *M. fascicularis.* Philippine *M. fascicularis* frequently occurs in primary evergreen rain forest, an uncommon habitat for non-Philippine *M. fascicularis.* Births in Philippine *M. fascicularis* probably peak in May. Taxonomically, pale to intermediate populations of Philippine macaques are referable to *M. f. fascicularis,* which also is distributed widely outside of the Philippines; dark populations are referable to *M. f. philippinensis,* which is endemic to the Philippines; mixed pale–intermediate–dark populations may be regarded as *M. f. fascicularis/M. f. philippinensis* contact-zone populations. Zoogeographic evidence suggests that ancestors of *M. f. philippinensis* dispersed to the Philippine archipelago from Borneo during the penultimate glacial maximum (ca. 160,000 years B.P.) and that ancestors of Philippine *M. f. fascicularis* dispersed to the archipelago from Borneo during the most recent glacial maximum (ca. 18,000 years B.P.); contact-zone populations probably are a product of interbreeding between these two successive waves of macaque dispersal from Borneo to the Philippines.

Acknowledgments

I thank curators and staff members of institutions listed in the Introduction for generous per-

mission to study specimens in their custody and for assistance in conducting the research. For valuable supplementary information, discussion, and help, I thank P. L. Alviola III (UPLBZD), J. E. Cadle (Academy of Natural Sciences, Philadelphia, Pennsylvania), W. G. Dee (Protected Areas and Wildlife Bureau, Quezon City, Philippines), E. Delson (AMNH), J. Erwin (Diagnon Corporation, Rockville, Maryland), P. Gonzales (PNM), C. O. Handley, Jr. (USNM), J.-J. Hwang (FMNH), P. D. Jenkins (BM(NH)), K. F. Koopman (AMNH), F.-W. Lange (SICONBREC), J. R. Leuterio (UPLBCF), P. Lowther (FMNH), J. B. Nazareno (SICONBREC), B. D. Patterson (FMNH), D. S. Rabor (UPLBCF), R. G. Resuello (SICONBREC), R. W. Thorington, Jr. (USNM), and W. C. Wozencraft (USNM). Special thanks are due L. R. Heaney (FMNH) for numerous helpful suggestions and for generously sharing his extensive knowledge of the Philippines and its mammalian fauna.

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Appendix 1: Specimens Examined

Total, 484 (Philippines, 352; Sabah, 132). Locality numbers (italicized) in parentheses; for details, see Gazetteer (Appendix 2) and figure 1.

Philippines

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***M. f. fascicularis*, 43**—MINDANAO: Gubat (*110*), FMNH 67725, 67729–67731; Libu (*110*), FMNH 67727–67728; Sigayan (*110*), FMNH 67722, 67732, 67740–67742; Situbo (*110*), FMNH 67719–67721, 67723–67724; Tacuta (*110*), FMNH 67733–67735; Tampalan (*110*), FMNH 67736; Canibongan (*111*), FMNH 67737–67739; Mamara (*112*), FMNH 67717–67718; Bucong (*113*), FMNH 65440–65444; Pulunbato, Mount (*117*), BM(NH) 1880.11.24.1; Zamboanga (*117*), USNM 144667–144668, 144698; San Ramon (*118*), FMNH 33507–33511. CAGAYAN SULU: Cagayan Sulu I. (*121*), USNM 125325. BASILAN: Isabela (*122*), USNM 125326; Camp No. 4–Camp No. 5, between (*123*), USNM 144665; Basilan I., E end (*125*), USNM 144666.

***M. f. philippinensis*, 55**—BALABAC: Minagas Point (*1*), USNM 477841. PALAWAN: Brookes Point (*3*), FMNH 62914, PNM 1197; Macagua (*3*), USNM 477849; Lapulapu (*4*), FMNH 62901; Puerto Princesa, E (*5*), FMNH 62902, 62905, 62913, FMNH 62903 (skull)/PNM 1191 (skin); Puerto Princesa, "Mt. wooded area" (*5*), USNM 333197; Tarabanan (*6*), USNM 477840, 477848. CULION: Makinis (*9*), PNM 1196; San Pedro (*9*), FMNH 62907–62908, PNM 1193–1995. MINDORO: Pinamalayan (*13*), MCZ 35059–35060, 35294; Pasi (*14*), MCZ 35295; Alag River (*17*), USNM 144674; Halcon, Mount (*18*), USNM 144675. LUZON: Lopez (*26*), BM(NH) 1899.1.8.1; Batangas (*28*), USNM 114140–114142; Mahayahaya (*29*), BM(NH) 1876.10.4.9; Maquiling, Mount (*33*), AMNH 175450, UPLBZD (unnumbered); Jalajala (*35*), MNHN 83/56; Bulacan Prov. (*38*), ZMB 5443; Data, Mount (*43*), BM(NH) 1897.5.2.1; Dimalasud Barrio (*44*), AMNH 187218; San Mariano Munic. (*44*), AMNH 187215–187217; Cagayan Valley (*46*), USNM 256071–256072; Barit (*47*), BM(NH) 1895.8.2.1; Lagañgilang (*49*), MCZ 35057–35058; Nagpartian (*52*), USNM 144676, 144678. SAMAR: Matuguinao (*55*), FMNH 87717–87719. LEYTE: Patoc Barrio (*62*), AMNH 187939–187940; Balinsasayo Barrio (*64*), AMNH 187936–187938. MINDANAO: Surigao (*82*), BM(NH) 1877.10.6.1; Agusan River (*84*), BM(NH) 1877.10.6.2.

***M. f. fascicularis*/*M. f. philippinensis* Contact Zone, 80**—NEGROS: Amio (*70*), FMNH 65452; Naliong (*70*), FMNH 67988–67993; Kabungahan (*71*), FMNH 65449–65451; Pamo-at (*72*), FMNH 65445–65448; Balangbang (*73*), FMNH 67996–67997; Kandomao (*73*), FMNH 67994–67995; Kauitan (*74*), FMNH 67998; Inubungan (*75*), FMNH 66327–66333; Buñga Barrio (*77*), UMMZ 161308; Balinsasayo, Lake, [N bank] (*78*), FMNH 66339–66348; Pamplona, 12 km S, 8 km W (*78*), UMMZ 157015; Pamplona, 18 km S (*78*), UMMZ 130418; Talinis (*78*), FMNH 75598–75603; Mabaja (*80*), FMNH 66334–66337. MINDANAO: Kamansi (*91*), FMNH 56493; Sumlog River (*92*), USNM 125323; McKinley, Mount, E slope, 4800 ft (*94*), FMNH 56161–56162, PNM 1184; Apo, Mount (*95*), USNM 125319–125322; Mainit, Mount Apo, 3800 ft (*95*), FMNH 61026; Matutungan (*96*), PNM 1185; Badiang (*97*), FMNH 56435; Pantod, Mount (*97*), PNM 1186; Burungkot (*102*), FMNH 56490, 56492, FMNH 56491 (skull)/PNM 1188 (skin); Bugusan (*103*), PNM 1187; Pantar (*106*), USNM 123448–123450, 123452–123456; Catagan (*108*), USNM 144671–144672, 144692, 144694, 144696–144697.

Probably *M. f. fascicularis*/M. f. philippinensis Contact Zone, 1—MINDANAO: Tangub (*107*), USNM 144669 (skin incomplete).

Subspecies undetermined, 10—BALUT: Balut I. (*120*), USNM 144664. ISLAND UNKNOWN (not mapped): ?Manila, RMNH 801; no locality, BM(NH) 1859.7.9.5, RMNH 1714, USNM 29680, 308725, 332896–332897, 344993–344994.

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***M. f. fascicularis*, 3**—MINDANAO: Zamboanga del Sur Prov. (not mapped), SICONBREC 1586 (living captive). TAWITAWI: Tawitawi I. (*127*), SICONBREC 1225, 1475 (living captives).

***M. f. philippinensis*, 15**—PALAWAN: Puerto Princesa (*5*), RMNH q, ZMB A4644; Puerto Princesa, E (*5*), PNM 1192. MINDORO: Bulalacao (*12*), USNM 151717; Calapan (*16*), AMNH 30595. LUZON: Maquiling, Mount (*33*), UPLBCF (unnumbered, 5 specimens); Jalajala (*35*), MNHN 80/1684; Daraitan, Mount (*36*), SICONBREC 100 (living captive); Manila (*37*), IRSN 9323, MNHN 373/265; no locality, RMNH 55.

Probably *M. f. philippinensis*, 1—MARIPIPI: Maripipi I. (*58*), UMMZ 156931 (in fluid).

***M. f. fascicularis*/*M. f. philippinensis* Contact Zone, 5**—NEGROS: Negros I., S (not mapped), BM(NH) 1872.8.20.5. MINDANAO: Busaw, Mount (*100*), PNM 1190; Maculi Point (*101*), AMNH 242092–242093; Pantar (*106*), USNM 123451.

Subspecies Undetermined, 10—BUSUANGA: Dimana (*10*), FMNH 62906. ISLAND UNKNOWN: AMNH 185134, BM(NH) 1939.622, FMNH 65453, MNHN 1880/634, RMNH 1447, UMMZ 102455, UPLBZD, (unnumbered), USNM 308724, 399509.

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***M. f. fascicularis*, 2**—MINDANAO: Zamboanga (*117*), ZMB A2920. JOLO: Crater Lake Mountain, foot (*126*), USNM 125324.

***M. f. philippinensis*, 30**—BALABAC: Minagas Point (*1*), USNM 477844–477846. PALAWAN: Mantalingajan, Mount (*2*), USNM 477843; Malabusog (*7*), USNM 477842; Palawan I. (not mapped), MNHN 83/1270. MINDORO: no locality, MMNH 4738. LUZON: Batangas (*28*), USNM 114139; Jalajala (*35*), MNHN 80/2460; Manila (*37*), NHRM M769; Massisiat (*50*), FMNH 62273–62276; Nagpartian (*52*), USNM 144679–144681, 144682 (fetus)–144687; Luzon I. (not mapped), ZMB 5442, ZMB (unnumbered). LEYTE: Baybay, 8.5 km N, 2.5 km E (*63*), UMMZ 151311; Pangasugan, Mount (*63*), USNM 458725–458726; Leyte I. (not mapped), USNM 282628. LEYTE OR SAMAR: no locality, USNM 277638.

Probably *M. f. philippinensis*, 14—MARIPIPI: Maripipi, 2 km N, 4 km W (*58*), USNM 458727; Maripipi I. (*58*), UMMZ 161312–161315, 161316 (mandible only), USNM 458728–458730, 458731 (mandible only), 458732–458734. BILIRAN: Sayao, Mount (*59*), USNM 458724.

***M. f. fascicularis*/*M. f. philippinensis* Contact Zone, 23**—NEGROS: Pagyabonan (*69*), FMNH 66338; Naliong (*70*), PNM (coll. nos. 525, 549, 597, 601); Balangbang (*73*), PNM (coll. no. 626); Kandomao (*73*), PNM (coll. no. 535); Balinsasayo, Lake (*78*), UMMZ 158623; Balinsasayo, Lake, 6 km N and 14 km W of Dumaguete City (*78*), UMMZ 161309; Pamplona, near (*79*), UMMZ 161310; Negros I., S (not mapped), SMTD B437, UMMZ 161317–161318, ZMB 1448. MINDANAO: Kamansi (*91*), PNM (coll. no. 1760); McKinley, Mount, E slope, 4800 ft (*94*), FMNH 56160; Caburan (*99*), PNM (coll. no. 1809); Maculi Point (*101*), AMNH 242094; Lanao, Lake (*105*), USNM 151661–151662; Catagan (*108*), USNM 144673, 144693, 144695.

Probably *M. f. fascicularis*/*M. f. philippinensis* Contact Zone, 8—MINDANAO: Tangub (*107*), USNM 144670; Masawan, Mount Malindang, 3500–4500 ft (*109*), FMNH 87428–87434.

Subspecies Undetermined, 52—BUSUANGA: San Nicolas (*11*), USNM 477847. SIBUYAN: Guitinguitin, Mount (*21*), FMNH 135714. PANAY: Calantas forest (*60*), FMNH 1172 (an unlabeled dark brown skin in MMNH, apparently the "Panay" skin listed by Timm & Birney, 1980, p. 568, may belong with this skull), MMNH 4740. BOHOL: Sandayong (*65*), FMNH 87419–87420, 87427; Cantaub (*66*), FMNH 87422–87426; Sandayong or Cantaub (*65* or *66*), FMNH 87421. CEBU: Cebu I. (*67*), SMTD 1069. ISLAND UNKNOWN: "Manila" (not mapped), AIUZ 18–19, 28–41, 341–343, 347–348, 350--352, 354, AS344–AS346, AS349, AS353; no locality, PNM (unnumbered, 2 specimens), USNM 144688–144689, 257991, 258587, 279563, 308723.

Sabah (Localities Not Mapped)

SKINS AND SKULLS, 66

M. f. fascicularis—BORNEO: Abai, MCZ, 21 specimens; Betotan, Sungai, ZRC, 1; Bongkabong, MCZ, 3; Bundu Tuhan, USNM, 2; Garau, MCZ, 4; Kadamaian, Sungai, MCZ, 1; Keningau, AMNH, 1; Kenokok, ZRC, 1; Kiau, MCZ, 2, ZRC, 2; Kiaulan, MCZ, 2; Kinabatangan, Sungai, USNM, 1; Kretam Besar, Sungai, FMNH, 1; Kretam Kechil, Sungai, FMNH, 1; Ranau, MCZ, 1, USNM, 5; Rayoh, Sungai, National Reference Collection, National University of Singapore, Singapore, 1; Rugading, MCZ, 1; Sapagaya Forest Reserve, FMNH, 2; Sibuga Besar, Sungai, FMNH, 1; Talibong, MCZ, 3; Tawao, AMNH, 1; Tenompok, Kampong, MCZ, 2; Tinonkok, MCZ, 1; Tuaran, MCZ, 5.

SKINS ONLY, 2

M. f. fascicularis—BORNEO: Papar, USNM, 1 specimen; Talibong, MCZ, 1.

SKULLS ONLY, 64

M. f. fascicularis—BORNEO: Abai, MCZ, 52 specimens; Bundu Tuhan, USNM, 2; Darvel Bay, ZMB, 1; Kinabalu, Mount, MCZ, 6; Lahad Datu, ZMB, 1; Sandakan, W, FMNH, 1; Segama, Sungai, ZMB, 1.

Appendix 2: Gazetteer

Locality names listed as primary entries in this gazetteer preferentially are official names approved by the U.S. Board on Geographic Names (USBGN Gazetteer: Philippine Islands, 1953). For Philippine macaque localities that are not included in the USBGN gazetteer, locality names are spelled here as in the original source. Secondary entries, with cross references to corresponding primary entries, indicate variant spellings or alternate locality names that appear on specimen tags, in published literature, or in unpublished manuscripts on Philippine macaques.

The sequence of information presented in primary entries is as follows:

1. Locality name;
2. Altitude, if reported by collector or observer;
3. Name of island and province;
4. Coordinates of locality (principal sources—USBGN Gazetteer; Census of the Philippines: 1960; Map of Negros Province, 1975; information in field notes of collector or observer);
5. Date of collection or observation;
6. Name of collector or observer;
7. Bibliographic reference (in parentheses) to published or unpublished locality notes, if any;
8. Abbreviated name of museum (see Introduction) where specimens are preserved;
9. Number of specimens available (with indication of part preserved, if skin and skull are not both present);
10. Abbreviated subspecific identification (*Mff* = *M. f. fascicularis*; *Mfp* = *M. f. philippinensis*; *Mff/Mfp* = *M. f. fascicularis/M. f. philippinensis* contact zone; subsp. indet. = subspecies undetermined);
11. Italicized locality number as shown in distribution map (fig. 1).

Abra Prov.; Luzon I.; 17°10′–18°00′N, 120°25′–121°05′E; reported by M. Buzeta and F. Bravo (1850, p. 265). *Mfp*; see *47–50.*

Abuyog. See Balinsasayo Barrio.

Agusan River, mouth; Mindanao I., Agusan del Norte Prov.; 9°00′N, 125°31′E; collected May 1877 by A. Everett (in Günther, 1879, p. 74); BM(NH), 1. *Mfp*; *84.*

Alag River, ca. 350 ft (= ca. 100 m); Mindoro I., Oriental Mindoro Prov.; ca. 13°22′N, 121°04′E; collected Nov. 1906 by E. A. Mearns (unpubl. MS., USNM); USNM, 1. *Mfp*; *17.*

Albay Prov.; Luzon I.; 13°00′–13°30′N, 123°15′–123°55′E; reported by Casto de Elera (1895, p. 3); specimen(s) in Museo de Santa Tomás, Manila (not seen). *Mfp*; *24.*

Amio, river bank, [< 1000 ft (= < 300 m)]; Negros I., Negros Oriental Prov.; ca. 9°24′N, 122°58′E; collected 13 May 1948 by D. S. Rabor; FMNH, 1 (second specimen—skin only—listed in FMNH catalog, not located). Altitude from A. L. Rand, unpublished sketch map and notes, FMNH. *Mff/Mfp*; *70.*

Apo, Mount, 6000 ft (= 1800 m); Mindanao I., Davao del Sur Prov.; ca. 6°59′N, 125°16′E; collected 25–29 June 1904 by E. A. Mearns (1905, p. 429); USNM, 4. Reported by R. E. Lewis (1988, p. 102). *Mff/Mfp*; *95.*

Arubal River, South Coast Range; Mindanao I., province unknown; not located; observed 30 Sep.–5 Oct. 1903 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; not mapped.

Aurora Memorial Park; Luzon I., Aurora Prov.; ca. 15°55′N, 121°30′E; reported by IUCN (1971, p. 390). *Mfp*; *42.*

Ayala; Mindanao I., Zamboanga del Sur; 6°57′N, 121°57′E; reported by J. B. Steere (1888b, p. 292). *Mff*; *118.*

Badiang, Tagabuli region, Santa Cruz Munic.; Mindanao I., Davao del Sur Prov.; ca. 6°49′N, 125°20′E; collected 9 Dec. 1946 by M. Celestino (see Hoogstraal, 1951, pp. 16, 24, 37); FMNH, 1. *Mff/Mfp*; *97.*

Baganga River, upper; Mindanao I., Davao Oriental Prov.; ca. 7°30′N, 126°30′E; observed 30 Apr. 1904 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; *87.*

Balabac I.; Palawan Prov.; 7°50′–8°05′N, 116°55′–117°05′E; reported by J. B. Steere (1888a, p. 144), possibly observed in Aug.–Sep. 1874 (see Sharpe, 1876, p. 297). *Mfp*; see *1.*

Balambing. See Balimbing.

Balangbang, Tolong (= Bayawan Munic.), [ca. 300 m]; Negros I., Negros Oriental Prov.; ca. 9°25′N, 122°52′E; collected 9–12 May 1950 by D. S. Rabor; FMNH, 2; PNM, 1 (skull only). Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989); altitude from A. L. Rand, unpublished sketch map and notes, FMNH. *Mff/Mfp*; *73.*

Balimbing; Tawitawi I., Tawitawi Prov.; 5°05′N, 119°57′E; unsuccessfully pursued 6 Jan. 1906 by L. Wood, Jr. and E. A. Mearns (unpubl. MS., USNM). *Mff*; *128.*

Balinsasayo Barrio, Abuyog Munic.; Leyte I., Leyte Prov.; 10°40′N, 124°57′E; collected 9–16 July 1961 by G. Alcasid and M. Celestino; AMNH, 3. *Mfp*; *64.*

Balinsasayo, Lake; Negros I., Negros Oriental Prov.; ca. 9°21′N, 123°10′E; reported in June 1981 by local residents (Heaney et al., 1981, pp. 123, 127). Collected 11 Aug. 1982 by P. D. Heideman; UMMZ, 1 (skull only). *Mff/Mfp*; *78.*

Balinsasayo, Lake, [N bank], 3500–4000 ft (= 1000–1200 m); Negros I., Negros Oriental Prov.; ca. 9°23′N, 123°04′E; collected 21 May–2 June 1949 by D. S. Rabor; FMNH, 10. Locality details from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mff/Mfp*; *78.*

Balinsasayo, Lake, 6 km N and 14 km W of Dumaguete City; Negros I., Negros Oriental Prov.; 9°22′N, 123°11′E; collected 2 Feb. 1984 by L. R. Heaney; UMMZ, 1 (skull only). *Mff/Mfp*; *78.*

Balit. See Barit.

Balut I., Sarangani Group; Davao del Sur Prov.; 5°20′–5°25′N, 125°20′–125°25′E; collected 23 Jan. 1906 by E. A. Mearns and Lt. Johnston; USNM, 1. Observed 6 Oct. 1906 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; *120*.

Banga I. See Banga, Port.

Banga, Port; Mindanao I., Zamboanga del Sur Prov.; 7°30′N, 122°26′E; observed 1 Feb. 1904 by E. A. Mearns (unpubl. MS., USNM) and L. Wood, Jr. *Mff*; *116*.

Banganan River, South Coast Range; Mindanao I., province unknown; not located; observed 30 Sep.–5 Oct. 1903 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; not mapped.

Bangued. See Lagañgilang.

Barit, 1000 ft (= 300 m); Luzon I., Abra Prov.; ca. 17°20′N, 120°42′E; collected 11 Nov. 1894 by J. Whitehead (1899, p. 84; also see Thomas, 1898, p. 381); BM(NH), 1. *Mfp*; *47*.

Basilan I.; Basilan Prov.; 6°25′–6°45′N, 121°45′–122°20′E; collected Oct.–Nov. 1874 by J. B. Steere (see Sharpe, 1876, p. 297; Günther, [1877], p. 735); museum unknown. Collected Nov. 1887 by J. B. Steere (1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). *Mff*; see *122–125*.

Basilan I., E end; Basilan Prov.; ca. 6°35′N, 122°15′E; collected 4 Feb. 1906 by E. A. Mearns (unpubl. MS., USNM), USNM, 1. *Mff*; *125*.

Baslut Island. See Balut I.

Bataan National Park; Luzon I., Bataan Prov.; ca. 14°30′N, 120°25′E; reported by IUCN (1971, p. 387). *Mfp*; *32*.

Bataan Prov.; Luzon I.; 14°25′–14°55′N, 120°15′–120°35′E; laboratory animals obtained 1960–1969 by Virus Laboratory of Institute of Public Health, University of Philippines, Manila (Famatiga, 1973, p. 316); apparently not preserved. *Mfp*; see *32*.

Batan I.; Batanes Prov.; 20°20′–20°30′N, 121°55′–122°05′E; monkeys absent 28 June–12 July 1989, apparently never present on this island (P. L. Alviola III, pers. comm., 4 Aug. 1989). Not mapped.

Batangas; Luzon I., Batangas Prov.; ca. 13°45′N, 121°03′E; collected in 1902 for U.S. Government Board Pan-American Exposition, Buffalo; USNM, 4 (1 skull only). *Mfp*; *28*.

Baybay, 8.5 km N, 2.5 km E, 500 m; Leyte I., Leyte Prov.; 10°46′N, 124°49′E; collected 26 May 1984 by L. R. Heaney; UMMZ, 1 (skull only). *Mfp*; *63*.

Bessang Pass National Park; Luzon I., Abra Prov.; ca. 17°20′N, 120°35′E; reported by IUCN (1971, p. 393). *Mfp*; *48*.

Biak-na-bato National Park; Luzon I., Bulacan Prov.; ca. 15°06′N, 121°04′E; reported by IUCN (1971, p. 391). *Mfp*; *39*.

Biliran I.; Leyte Prov.; 11°30′–11°45′N, 124°20′–124°35′E; reported by L. R. Heaney (1986, p. 132), based on specimen(s) in UMMZ (not located by me in Oct. 1989). Probably *Mfp*; see *59*.

Bilukan. See Bulacan.

Bohol I. See Cantaub and Sandayong.

Brookes Point; Palawan I., Palawan Prov.; 8°47′N, 117°50′E; collected 10–11 May 1947 by D. S. Rabor (see Hoogstraal, 1951, p. 76); FMNH, 1; PNM, 1. *Mfp*; *3*.

Bucong (? = Bukon), Pagadian region; Mindanao I., Zamboanga del Sur Prov.; ca. 7°54′N, 123°30′E; collected 15–18 June 1948 by D. S. Rabor; FMNH, 5. *Mff*; *113*.

Bugusan, 50 ft (= 15 m), Parang Munic.; Mindanao I., Maguindanao Prov.; 7°27′N, 124°14′E; collected 9 Dec. 1946 by G. L. Alcasid and P. Añonuevo (see Hoogstraal, 1951, p. 62); PNM, 1. *Mff/Mfp*; *103*.

Bukon. See Bucong.

Bulacan Prov.; Luzon I.; 14°40′–15°15′N, 120°40′–121°15′E; collected Jan.–Mar. 1872 by A. B. Meyer (1896, p. 4; also see Walden, 1875, p. 125); ZMB, 1. *Mfp*; *38*.

Bulalacao; Mindoro I., Oriental Mindoro Prov.; 12°20′N, 121°20′E; collected 17 Oct. 1906 by Dr. Porter; USNM, 1 (skin only). *Mfp*; *12*.

Bulalacca. See Bulalacao.

Buñga Barrio, Dauin Munic., W; Negros I., Negros Oriental Prov.; 9°12′N, 123°16′E; collected Apr. 1984 by L. R. Heaney; UMMZ, 1. *Mff/Mfp*; *77*.

Burungkot, Upi Munic.; Mindanao I., Maguindanao Prov.; collected 7–8 Jan. 1947 by F. Werner, A. Gabriel, and P. Añonuevo (see Hoogstraal, 1951, pp. 62, 65); FMNH, 2; FMNH (skull) and PNM (skin), 1. *Mff/Mfp*; *102*.

Busaw, Mount, ca. 500 ft (= 150 m); Mindanao I., Davao del Sur Prov.; ca. 5°54′N, 125°36′E; collected 26 Jan. 1947 by H. Hoogstraal (1951, pp. 37, 62); PNM, 1 (skin only). *Mff/Mfp*; *100*.

Busuanga. See Dimana and San Nicolas.

Busuanga I.; Palawan Prov.; 11°55′–12°20′N, 119°50′–120°20′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; see *10–11*.

Butuan River. See Agusan River.

Cabasaran River. See Kabasalan River.

Caburan, near sea level; Mindanao I., Davao del Sur Prov.; ca. 5°55′N, 125°39′E; collected 13

Jan. 1947 by H. Hoogstraal (1951, p. 60); PNM, 1 (skull only). *Mff/Mfp*; *99*.

Cagayan Sulu I.; Tawitawi Prov.; 7°00′–7°05′N, 118°25′–118°35′E; collected 25 Feb. 1904 by E. A. Mearns (1905, p. 431; unpubl. MS., USNM); USNM, 1. *Mff*; *121*.

Cagayan Valley; Luzon I., Cagayan Prov. or Isabela Prov.; 16°30′–18°20′N, 121°35′–121°55′E; captured 14 Jan. 1931 for National Zoological Park; USNM, 2. *Mfp*; *46*.

Calamianes. See Culion, Dimana, and San Nicolas.

Calantas forest; Panay I., Capiz Prov.; ca. 11°30′N, 122°25′E; collected 11–21 Nov. 1890 by D. C. Worcester and F. S. Bourns (Worcester, 1898, p. 243; Worcester & Bourns, 1898, map; [1905], pp. 135, 137); FMNH, 1 (skull only; an unlabeled dark brown skin in MMNH, apparently the "Panay" skin listed by Timm & Birney, 1980, p. 568, may belong with this skull); MMNH, 1 (skeleton only). Subsp. indet.; *60*.

Calapan; Mindoro I., Oriental Mindoro Prov.; 13°25′N, 121°10′E; collected 19 Oct. 1909 by R. C. Andrews (1911, p. 21); AMNH, 1 (skin only). *Mfp*; *16*.

Camansi. See Kamansi.

Camp No. 2. See Alag River.

Camp No. 2–Camp No. 3, between; Basilan I. (NW), Basilan Prov.; ca. 6°40′N, 121°50′E; observed 29 Jan. 1906 by E. A. Mearns (unpubl. MS., USNM). *Mff*; *123*.

Camp No. 4—Camp No. 5, between; Basilan I. (NW), Basilan Prov.; ca. 6°40′N, 121°50′E; collected 31 Jan. 1906 by E. A. Mearns (unpubl. MS., USNM); USNM, 1. *Mff*; *123*.

Camp No. 6. See Halcon, Mount.

Camp No. 6–Camp No. 7, between. See Tiputipu, near.

Camp Pantar. See Pantar.

Camp Vicars–Malabang, between; Mindanao I., Lanao del Sur Prov.; ca. 7°40′N, 124°05′E; observed 11 Apr. 1904 by E. A. Mearns (unpubl. MS., USNM). *Mff/Mfp*; *104*.

Candomao. See Kandomao.

Canibongan, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; 8°25′N, 123°13′E; collected 5 June 1950 by D. S. Rabor; FMNH, 3. *Mff*; *111*.

Canlaon National Park; Negros I., Negros Occidental Prov.; ca. 10°25′N, 123°08′E; reported by IUCN (1971, p. 387). Subsp. indet.; *68*.

Canlaon Volcano, 6000 ft (= 1800 m); Negros I., Negros Occidental Prov.; ca. 10°25′N, 123°08′E; observed Jan.–Aug. 1896 by J. Whitehead (1899, p. 85; in Thomas, 1898, p. 381). Subsp. indet.; *68*.

Canloön Volcano. See Canlaon Volcano.

Cantaub, 700–750 m, Sierra-Bullones Munic.; Bohol I., Bohol Prov.; ca. 9°48′N, 124°18′E; collected 14–29 Apr. 1955 by D. S. Rabor (pers. comm., 4 Aug. 1989; see also Rand & Rabor, 1960, p. 312), FMNH, 5 (skulls only). Subsp. indet.; *66*.

Caraga [Munic.]; Mindanao I., Davao Oriental Prov.; ca. 7°20′N, 126°34′E; reported by M. Buzeta and F. Bravo (1850, p. 505). Subsp. indet.; *89*.

Catagan [vicinity], 1100–5750 ft (= 335–1750 m); Mindanao I., Misamis Occidental Prov.; ca. 8°10′N, 123°40′E; collected 10–25 May 1906 by E. A. Mearns (unpubl. MS., USNM) and R. A. Schroder (in Rand & Rabor, 1960, p. 262); USNM, 9 (3 skulls only). *Mff/Mfp*; *108*.

Catanduanes I.; Catanduanes Prov.; 13°30′–14°05′N, 124°00′–124°25′E; observed 1968–1971 by P. C. Gonzales (see Heaney et al., in prep.). Reported as present in 1988 by local hunters (Heaney et al., in prep.). *Mfp*; *53*.

Cateel River and Agusan River, crest between; Mindanao I., Davao Prov.; 7°40′N, 126°10′E; observed 3 May 1904 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; *86*.

Cateel River, lower; Mindanao I., Davao Oriental Prov.; ca. 7°48′N, 126°27′E; collected 5 Oct. 1906 by L. Wood, Jr. (see E. A. Mearns, unpubl. MS., USNM); specimen not located (not in USNM catalog). Subsp. indet.; *88*.

Catubig River, between Laguan (= ?Laoang) and Catubig; Samar I., Northern Samar Prov.; ca. 12°30′N, 125°02′E; observed 1 Oct. 1906 by E. A. Mearns (unpubl. MS., USNM). *Mfp*; *54*.

Cavite. See Santa Cruz.

Cavite Prov.; Luzon I.; 14°05′–14°30′N, 120°35′–121°05′E; laboratory animals obtained 1960–1969 by Virus Laboratory of Institute of Public Health, University of Philippines, Manila (Famatiga, 1973, p. 316); apparently not preserved. *Mfp*; see *31*.

Cawitan. See Kauitan.

Cebu I.; Cebu Prov.; 9°25′–11°15′N, 123°20′–124°05′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Collected before 1896 by unknown collector (see Meyer, 1896, p. 4); SMTD, 1 (skull only). Subsp. indet.; *67*.

Concepcion. See Tarabanan.

Cotabato. See Bugasan and Burungkot.

Culion I.; Palawan Prov.; 11°35′–12°00′N, 119°50′–

120°05′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). *Mfp*; see *9*.

Crater Lake Mountain, foot; Jolo I., Sulu Prov.; ca. 5°58′N, 121°10′E; collected 16 Nov. 1903 by E. A. Mearns (1905, p. 430; unpubl. MS., USNM); USNM, 1 (skull only). *Mff*; *126*.

Dagami Munic. See Patoc Barrio.

Dalawan Bay. See Minagas Point.

Daraitan, Mount, Tanay Munic.; Luzon I., Rizal Prov.; 14°37′N, 121°24′E; captive obtained 28 Feb. 1984; SICONBREC, 1 (captive examined 4 Aug. 1989). *Mfp*; *36*.

Data, Mount, 7500 ft (= 2300 m); Luzon I., Benguet Prov.; ca. 16°51′N, 120°52′E; collected Feb. 1895 by J. Whitehead (1899, p. 84; in Thomas, 1898, p. 379; cf. Hoogstraal, 1951, p. 30; Rabor, 1955, p. 195); BM(NH), 1. *Mfp*; *43*.

Datu Anib's place. See Catagan [vicinity].

Davao Gulf. See Sumlog River.

Davao Prov., Davao del Sur Prov., or Davao Oriental Prov.; Mindanao I.; 5°35′–8°00′N, 125°05′–126°35′E; laboratory animals obtained 1960–1969 by Virus Laboratory of Institute of Public Health, University of Philippines, Manila (Famatiga, 1973, p. 316); apparently not preserved. Subsp. indet.; see *86–100*.

Dimalasud Barrio, San Mariano Munic., Sierra Madre; Luzon I., Isabela Prov.; ca. 17°00′N, 122°00′E; collected 19 May 1961 by American–Philippine Expedition; AMNH, 1. For locality data, see AMNH catalog, nos. 187121, 187125, 187179, 187180. *Mfp*; *44*.

Dimana; Busuanga I., Palawan Prov.; ca. 12°03′N, 120°08′E; collected 20 Mar. 1947 by D. S. Rabor (pers. comm., 4 Aug. 1989; also see Hoogstraal, 1951, p. 81); FMNH, 1 (skin only). Subsp. indet.; *10*.

Dimaniang. See Dimana.

Dinagat I.; Surigao del Norte Prov.; 9°50′–10°30′N, 125°30′–125°40′E; no monkeys seen 21 Apr. 1904 (E. A. Mearns, unpubl. MS., USNM). Monkeys not included in mammalian faunal list published by L. R. Heaney and D. S. Rabor (1982, p. 16). Not mapped.

Disabungan River. See San Mariano Munic.

Dulungan, Monte. See Halcon, Mount.

Fuyot Spring National Park; Luzon I., Isabela Prov.; ca. 17°10′N, 122°10′E; reported by IUCN (1971, p. 392). *Mfp*; *45*.

Gubat, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 28 May–1 June 1950 by D. S. Rabor; FMNH, 4. *Mff*; *110*.

Guimaras I.; 10°25′–10°45′N, 122°25′–122°45′E; Iloilo Prov.; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; *61*.

Guitinguitin, Mount; Sibuyan I., Romblon Prov.; 12°25′N, 122°34′E; captive obtained 3 June 1989 by S. M. Goodman (mother of captive shot by local resident at least 5 years previously; captive then a nursling); FMNH, 1 (skeleton only). Subsp. indet.; *21*.

Halcon, Mount, 6000 ft (= 1800 m); Mindoro I., Oriental Mindoro Prov.; ca. 13°16′N, 121°00′E; observed Oct. 1895–Jan. 1896 by J. Whitehead (1899, p. 85; in Thomas, 1898, p. 381). *Mfp*; *18*.

Halcon, Mount, spur of main ridge, 6300 ft (= 1900 m); Mindoro I., Oriental Mindoro Prov.; ca. 13°16′N, 121°00′E; collected 21 Nov. 1906 by Señor Estrellus and E. A. Mearns (unpubl. MS., USNM); USNM, 1. *Mfp*; *18*.

Ifugao. See Data, Mount.

Inobongan. See Inubungan.

Inubungan, Santa Catalina Barrio Sitio; Negros I., Negros Oriental Prov.; ca. 9°23′N, 122°57′E; collected 20–28 Dec. 1948 by D. S. Rabor; FMNH, 7. *Mff/Mfp*; *75*.

Isabela, near; Basilan I., Basilan Prov.; ca. 6°42′N, 121°58′E; collected 26 Jan. 1904 by E. A. Mearns; USNM, 1. *Mff*; *122*.

Isabella. See Isabela, near.

Iwahig. See Lapulapu.

Jalajala; Luzon I., Laguna Prov. or Rizal Prov.; ca. 14°21′N, 121°19′E; shot as agricultural pest 1819–1839 by P. P. de La Gironiere ([1853?], p. 193). Collected Feb. 1880 (and possibly other dates) by A. Marche (1970 translation, p. 59); MNHN, 3 (1 skull only, 1 skull in skin). *Mfp*; *35*.

Jolo I.; Sulu Prov.; 5°50′–6°05′N, 120°50′–121°25′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). *Mff*; see *126*.

Kabasalan River; Mindanao I., Zamboanga del Sur Prov.; ca. 7°46′N, 122°46′E; observed 30–31 Jan. 1904 by E. A. Mearns (unpubl. MS., USNM). *Mff*; *114*.

Kabongakan. See Kabungahan.

Kabungahan, Amio region; Negros I., Negros Oriental Prov.; ca. 9°30′N, 122°46′E; collected 11 May 1948 by D. S. Rabor; FMNH, 3. Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mff/Mfp*; *71*.

Kamansi, Mati region; Mindanao I., Davao Oriental Prov.; 6°56′N, 126°11′E; collected 29 Dec. 1946 by P. Convocar (see Hoogstraal, 1951, pp.

37, 59); FMNH, 1; PNM, 1 (skull only). *Mff/Mfp*; *91.*

Kandomao, Tolong (= Bayawan Munic.); Negros I., Negros Oriental Prov.; ca. 9°23′N, 122°52′E; collected 14 Apr. 1950 by D. S. Rabor; FMNH, 2; PNM, 1 (skull only). Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mff/Mfp*; *73.*

Katipunan. See Canibongan, Gubat, Libu, Mamara, Sigayan, Situbo, Tacuta, and Tampalan.

Kauitan, Santa Catalina Barrio Sitio; Negros I., Negros Oriental Prov.; 9°18′N, 122°53′E; collected 7 July 1950 by D. S. Rabor and T. Zamora; FMNH, 1. *Mff/Mfp*; *74.*

Kibawalan, Malalag Munic., 1200–2200 ft (= 365–670 m); Mindanao I., Davao del Sur Prov.; ca. 6°20′N, 125°20′E; observed 29 May 1964 by R. B. Gonzales (1968, p. 483). *Mff/Mfp*; *98.*

Kraan Point. See Maculi Point.

Lagañgilang; Luzon I., Abra Prov.; 17°37′N, 120°44′E; collected 30 Jan. 1937 by B. Lawrence (see Barbour, 1939, p. 26); MCZ, 2. *Mfp*; *49.*

Laguan. See Catubig River.

Laguna Prov.; Luzon I.; 14°00′–14°35′N, 121°00′–121°35′E; reported by Casto de Elera (1895, p. 3); specimen(s) in Museo de Santa Tomás, Manila (not seen). *Mfp*; see *33–35.*

Lanao, Lake; Mindanao I., Lanao del Sur Prov.; ca. 7°53′N, 124°15′E; collected before 1913 by G. C. Lewis; USNM, 2 (skulls only). *Mff/Mfp*; *105.*

Laoag, N; Luzon I., Ilocos Norte Prov.; ca. 18°12′N, 120°36′E; observed 7 Feb. 1907 by E. A. Mearns (unpubl. MS., USNM). *Mfp*; *51.*

Laoang. See Catubig River.

Laoog. See Laoag, N.

Lapulapu; Palawan I., Palawan Prov.; ca. 9°45′N, 118°39′E; collected 2 Mar. 1947 by D. S. Rabor and F. Werner (see Hoogstraal, 1951, p. 75); FMNH, 1. *Mfp*; *4.*

La Union, Cabadbaran Munic.; Mindanao I., Agusan del Norte Prov.; 9°05′N, 125°32′E; collected 1951–1952 by F. Salomonsen (see Sanborn, 1953, p. 285); Zoologisk Museum, Copenhagen, 1 (not seen). *Mfp*; *83.*

Lepanto. See Data, Mount.

Leyte I.; province unknown; 10°00′–11°35′N, 124°15′–125°15′E; collected Apr. 1888 by J. B. Steere (1890, pp. 5, 28); museum unknown. Collected 1944–1945 by C. O. Mohr; USNM, 1 (skull only). *Mfp*; see *62–64.*

Libu, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 30 May 1950 by D. S. Rabor; FMNH, 2. *Mff*; *110.*

Lopez; Luzon I., Quezon Prov.; 13°53′N, 122°15′E; collected before 1899 by A. Everett; BM(NH), 1. *Mfp*; *26.*

Los Baños; Luzon I., Laguna Prov.; 14°13′N, 121°11′E; observed May 1861 by E. von Martens (1876, pp. 193, 200). *Mfp*; *34.*

Luçon. See Luzon I.

Luzon I.; province unknown; 12°30′–18°40′N, 119°45′–124°15′E; collected in 1865 by [J.] Verreaux; RMNH, 1 (skin only). Obtained in Paris, "some years" before 1867, by J. H. Slack (1867, p. 36); skin and skull formerly in Academy of Natural Sciences, Philadelphia, now lost (J. E. Cadle, letter, 14 Nov. 1989). Collected Jan.–Mar. 1872 by A. B. Meyer (1896, p. 4; also see Walden, 1875, p. 125); ZMB, 2 (skulls only). Collected July 1888 by J. B. Steere (1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Reported by Casto de Elera (1895, p. 3); specimen(s) in Museo de Santa Tomás, Manila (not seen). *Mfp*; see *24–52.*

Mabaha. See Mabaja.

Mabaja, Bais City; Negros I., Negros Oriental Prov.; ca. 9°39′N, 123°01′E; collected 21–26 Apr. 1949 by D. S. Rabor; FMNH, 4. *Mff/Mfp*; *80.*

Macagua, 250 ft (= 75 m), Brookes Point Barrio; Palawan I., Palawan Prov.; ca. 8°47′N, 117°49′E; collected 19 Apr. 1962 by D. S. Rabor; USNM, 1. Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mfp*; *3.*

Maculi Point, Cotabato coast; Mindanao I., Sultan Kudarat Prov.; 6°07′N, 124°19′E; collected 1920–1923 by E. H. Taylor (1934, p. 341); AMNH, 3 (2 skins only, 1 skull only). *Mff/Mfp*; *101.*

Mahayahaya, mountains of; Luzon I., Batangas Prov.; ca. 13°55′N, 120°52′E; collected May–July 1874 by J. B. Steere (see Sharpe, 1876, p. 297; Günther, [1877], p. 735); BM(NH), 1. *Mfp*; *29.*

Mahayhay. See Mahayahaya.

Mainit Hot Spring National Park; Mindanao I., Agusan del Sur Prov.; ca. 8°20′N, 125°35′E; reported by IUCN (1971, p. 391). Subsp. indet.; *85.*

Mainit, Mount Apo, 3800 ft (= 1150 m); Mindanao I., Davao del Sur Prov.; collected 17 Nov. 1946 by H. Hoogstraal (1951, p. 56); FMNH, 1. *Mff/Mfp*; *95.*

Makiling, Mount. See Maquiling, Mount.

Makinis; Culion I., Palawan Prov.; ca. 11°51′N, 120°01′E; collected 29 Mar. 1947 by P. Añonu-

evo (see Hoogstraal, 1951, p. 83); PNM, 1. *Mfp*; 9.

Malabang. See Camp Vicars–Malabang.

Malabusog, Tinitian Barrio; Palawan I., Palawan Prov.; ca. 10°04′N, 119°07′E; collected 29 Apr. 1962 by M. C. Thompson (see BBM field catalog); USNM, 1 (skull only). Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mfp*; *7*.

Malampaya Sound, rocky shore; Palawan I., Palawan Prov.; ca. 10°51′N, 119°20′E; observed 12 Sep. 1906 by P. C. Frier et al. (see E. A. Mearns, unpubl. MS., USNM). *Mfp*; *8*.

Malindang, Mount. See Catagan and Masawan.

Mamara, Katipunan Munic., 2500 ft (= 750 m); Mindanao I., Zamboanga del Norte Prov.; collected 21 May 1950 by D. S. Rabor; FMNH, 2. *Mff*; *112*.

Manay River, above Manay; Mindanao I., Davao Oriental Prov.; ca. 7°13′N, 126°32′E; collected 6 Oct. 1906 by L. Wood, Jr. (see E. A. Mearns, unpubl. MS., USNM); museum unknown, 2 (skulls only; not seen; not listed in USNM catalog). Subsp. indet.; *90*.

Manila; Luzon I., National Capital Region; ca. 14°35′N, 121°00′E; collected in 1841 by Kapten Nisser; NHRM, 1 (skull only). Living captive presented 6 Aug. 1841 to Ménagerie, MNHN, by A. Chenest (see I. Geoffroy, [1843], p. 570); MNHN, 1 (skin only). Collected in 1845 by Dechange; IRSN, 1 (skin only). *Mfp*; *37*.

"Manila"; island and province unknown; living captive received 8 Jan. 1916; RMNH, 1. Received (date unknown) from C. W. Stiles; AIUZ, 30 (skulls and skeletons only). Subsp. indet.; not mapped.

Manille. See Manila.

Mantalingajan, Mount; Palawan I., Palawan Prov.; 8°48′N, 117°40′E; collected 11 Apr. 1962 by M. C. Thompson (see Kuntz, 1969, p. 208); USNM, 1 (skull only). *Mfp*; *2*.

Manuk Manka I.; Tawitawi Prov.; 4°48′–4°50′N, 119°48′–119°52′E; monkeys absent 6 Jan. 1906 (E. A. Mearns, unpubl. MS., USNM). Not mapped.

Maquiling, Mount, Los Baños Munic.; Luzon I., Laguna Prov.; 14°08′N, 121°12′E; collected 16 Feb. 1921 by J. T. Zimmer; AMNH, 1. Collected 29 Nov. 1947 by R. M. Sojetado; UPLBZD, 1. Collected 1977–1980 by J. Leuterio (pers. comm., 31 July 1989); UPLBCF, 5 (skins only). *Mfp*; *33*.

Marinduque I.; Marinduque Prov.; 13°10′–13°35′N, 121°50′–122°10′E; reported by D. Sánchez y Sánchez (1900, p. 288). Probably *Mfp*; *23*.

Maripipi, 2 km N, 3 km W, 650 m; Maripipi I., Leyte Prov.; 11°47′N, 124°19′E; troop heard in 1987 by E. A. Rickart et al. (in prep.). Probably *Mfp*; *58*.

Maripipi, 2 km N, 4 km W, 200 m; Maripipi I., Leyte Prov.; 11°47′N, 124°18′E; collected 20 Apr. 1987 by P. D. Heideman; USNM, 1 (skull only). Probably *Mfp*; *58*.

Maripipi I.; Leyte Prov.; 11°45′–11°50′N, 124°15′–124°20′E; collected 4–7 July 1981 by L. R. Heaney; UMMZ, 1 (in fluid). Collected 8 May 1984 by P. D. Heideman; UMMZ, 5 (4 skulls only, 1 mandible only). Collected 22–25 Apr. 1987 by P. D. Heideman; USNM, 7 (6 skulls only, 1 mandible only). Probably *Mfp*; *58*.

Masawan, Mount Malindang, 3500–4500 ft (= 1000–1400 m); Mindanao I., Misamis Occidental Prov.; ca. 8°20′N, 123°36′E; collected 2–9 Apr. 1956 by D. S. Rabor (see Rand & Rabor, 1960, pp. 269, 273; pers. comm., 4 Aug. 1989); 7 (skulls only). Probably *Mff/Mfp*; *109*.

Masawan, Mount Malindang, 4400–5000 ft (= 1340–1520 m); Mindanao I., Misamis Occidental Prov.; ca. 8°20′N, 123°36′E; collected 25 Dec. 1962 by D. S. Rabor (see Rand & Rabor, 1960, pp. 269, 273); museum unknown, 1 (not seen, listed in BBM field catalog). Probably *Mff/Mfp*; *109*.

Masbate I.; Masbate Prov.; 11°45′–12°35′N, 123°10′–124°05′E; reported by D. Sánchez y Sánchez (1900, p. 288). Subsp. indet.; *22*.

Massisiat, 3500 ft (= 1000 m); Luzon I., Abra Prov.; ca. 17°35′N, 120°55′E; collected 14–19 May 1946 by D. S. Rabor (1955, p. 197; also see Hoogstraal, 1951, p. 32), M. Celestino, A. Castro, H. R. Rabanal, and G. Alcasid; 4 (skeletons only). *Mfp*; *50*.

Matchin. See Jalajala.

Mati. See Kamansi.

Matuguinao; Samar I., Western Samar Prov.; 12°08′N, 124°53′E; collected 11–21 Apr. 1957 by D. S. Rabor; FMNH, 3. *Mfp*; *55*.

Matutungan, Tagabuli region, Santa Cruz Munic., 2500 ft (= 760 m); Mindanao I., Davao del Sur Prov.; ca. 6°51′N, 125°18′E; collected 10 Dec. 1946 by M. Celestino (see Hoogstraal, 1951, pp. 24, 37); PNM, 1. *Mff/Mfp*; *97*.

McKinley, Mount, E slope, 4800 ft (= 1460 m), 5700 ft (= 1740 m), 5800 ft (= 1770 m); Mindanao I., Davao del Sur Prov.; ca. 7°06′N, 125°20′E; collected 20 Aug.–4 Sep. 1946 by H. Hoogstraal (1951, pp. 37, 45, 49); FMNH, 3 (1 skeleton only); PNM, 1. *Mff/Mfp*; *94*.

McKinley, Mount, E slope, 6400 ft (= 1950 m);

Mindanao I., Davao del Sur Prov.; ca. 7°06′N, 125°20′E; observed 1–12 Sep. 1946 by H. Hoogstraal (1951, pp. 37, 45, 49). *Mff/Mfp*; *94.*

Minagas Point, Dalawan Bay; Balabac I., Palawan Prov.; 7°54′N, 117°05′E; collected 22–25 Apr. 1962 by M. C. Thompson and R. Gonzales (see BBM field catalog); USNM, 4 (3 skulls only). *Mfp*; *1.*

Mindanao I.; province unknown; 5°35′–9°50′N, 121°55′–126°40′E; collected Oct.–Dec. 1887 by J. B. Steere (1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; see *82–118.*

Mindoro I.; province unknown; 12°10′–13°30′N, 120°15′–121°35′E; collected 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61); MMNH, 1 (skeleton only). *Mfp*; see *12–18.*

Monte Data. See Data, Mount.

Monte Pulumbato. See Pulunbato, Mount.

Mount Isarog National Park; Luzon I., Camarines Sur Prov.; ca. 13°39′N, 123°23′E; reported by IUCN (1971, p. 388). *Mfp*; *25.*

Nagpartian, ca. 400 ft (= 120 m); Luzon I., Ilocos Norte Prov.; 18°31′N, 120°40′E; collected 24 Feb.–2 Mar. 1907 by E. A. Mearns; USNM, 11 (9 skulls only). One additional specimen (USNM 144677, skin and skull) from this series was transferred in 1936 to the Bureau of Science, Manila (USNM catalog); this specimen probably was destroyed during World War II (see Hoogstraal, 1951, p. 9). *Mfp*; *52.*

Naliong, Tolong (= Bayawan Munic.), [500–800 m]; Negros I., Negros Oriental Prov.; ca. 9°26′N, 122°52′E; collected 21 Apr.–1 May 1950 by D. S. Rabor; FMNH, 6; PNM, 4 (skulls only). Altitude and coordinates from A. L. Rand, unpublished sketch map and notes, FMNH. *Mff/Mfp*; *70.*

Naujan Lake National Park; Mindoro I., Oriental Mindoro Prov.; ca. 13°10′N, 121°21′E; reported by IUCN (1971, p. 390). *Mfp*; *15.*

Naval, 5 km N, 10 km E, 800 m, 850 m; Biliran I., Leyte Prov.; 11°36′N, 124°29′E; observed 18 Apr. 1987 and another unknown date in 1987 by E. A. Rickart et al. (in prep.; L. R. Heaney, FMNH, field notes). Probably *Mfp*; *59.*

Negros I.; province unknown; 9°05′–11°00′N, 122°20′–123°35′E; collected Feb. 1888 by J. B. Steere (1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; see *68–80.*

Negros I., S; province unknown; coordinates unknown; collected about 1872 by A. B. Meyer (1896, p. 4); BM(NH), 1 (skull not seen); SMTD, 1 (skull only); ZMB, 1 (skull only). Collected June 1984 by P. D. Heideman; UMMZ, 2 (skulls only). *Mff/Mfp*; see *69–80.*

Nituna River, South Coast Range; Mindanao I., province unknown; not located; observed 30 Sep.–5 Oct. 1903 by E. A. Mearns (unpubl. MS., USNM). Subsp. indet.; not mapped.

Pagadian. See Bucong (? = Bukon).

Pagyabonan, Bais City; Negros I., Negros Oriental Prov.; ca. 9°41′N, 122°59′E; collected 14 May 1949 by D. S. Rabor; FMNH, 1 (skull only). *Mff/Mfp*; *69.*

Palawan I.; Palawan Prov.; 8°20′–11°25′N, 117°10′–119°45′E; collected in 1883 by A. Marche (1970 translation, p. 203); MNHN, 1 (skull only). Collected Aug.–Sep. 1887 by J. B. Steere (1888a, p. 143; 1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Reported by B. D. Cabrera (1973, p. 251). *Mfp*; see *2–8.*

Pamo-at, Amio region; Negros I., Negros Oriental Prov.; ca. 9°30′N, 122°41′E; collected 28 Apr.–6 May 1948 by D. S. Rabor; FMNH, 4. Coordinates from J. R. Leuterio, UPLBCF (pers. comm., 31 July 1989). *Mff/Mfp*; *72.*

Pamplona, 12 km S, 8 km W, 840 m; Negros I., Negros Oriental Prov.; ca. 9°22′N, 123°03′E; collected June 1981 by P. D. Heideman; UMMZ, 1. *Mff/Mfp*; *78.*

Pamplona, 18 km S; Negros I., Negros Oriental Prov.; ca. 9°18′N, 123°07′E; collected 8 June 1979 by K. M. Mudar; UMMZ, 1. *Mff/Mfp*; *78.*

Pamplona, near; Negros I., Negros Oriental Prov.; ca. 9°30′N, 123°07′E; collected 22 Apr. 1984 by L. R. Heaney; UMMZ, 1 (skull only). *Mff/Mfp*; *79.*

Panay. See Calantas forest.

Panay I.; province unknown; 10°25′–11°55′N, 121°50′–123°10′E; reported origin of zoo animal observed in Manila in 1923 by E. H. Taylor (1934, p. 336). Subsp. indet.; see *60.*

Pangapuyan I.; Zamboanga del Sur Prov.; 6°54′–6°55′N, 122°10′–122°11′E; observed 2 Feb. 1904 by E. A. Mearns (unpubl. MS., USNM). *Mff*; *119.*

Pangasinan Prov.; Luzon I.; 15°35′–16°15′N, 119°45′–120°55′E; albino(s) reported by R. P. Casto de Elera (1895, p. 2). *Mfp*; *41.*

Pangasugan, Mount; Leyte I., Leyte Prov.; 10°46′N, 124°49′E; collected Apr. 1987 by L. R. Heaney; USNM, 2 (skulls only). *Mfp*; *63.*

Pangasugan, Mount, 300 m, 500 m, 700 m; Leyte I., Leyte Prov.; 10°46′N, 124°49′E; observed 2

Mar.–13 Apr. 1987 by E. A. Rickart et al. (in prep.). *Mfp*; *63.*

Panguil Bay. See Tangub.

Pantar, 1900 ft (= 580 m); Mindanao I., Lanao del Norte Prov.; 8°04′N, 124°14′E; collected 13 Aug.–20 Sep. 1903 by E. A. Mearns (1905, pp. 428, 433); USNM, 9 (1 skin only). *Mff/Mfp*; *106.*

Pantod, Mount, Tagabuli region, Santa Cruz Munic., 2500 ft (= 760 m); Mindanao I., Davao del Sur Prov.; ca. 6°49′N, 125°20′E; collected 12 Dec. 1946 by M. Celestino (see Hoogstraal, 1951, pp. 20, 24, 37); PNM, 1. *Mff/Mfp*; *97.*

Panyabunan. See Pagyabonan.

Paragua. See Palawan I.

Parak Creek, Tudaya, 1 km N, 700–1200 m; Mindanao I., Davao del Sur Prov.; ca. 6°58′N, 125°22′E; observed as prey of eagle 16 Feb. 1973 by R. S. Kennedy (1977, p. 5). *Mff/Mfp*; *93.*

Parang. See Bugasan.

Pasananca. See Pulunbato, Mount.

Pasi, Pola Munic.; Mindoro I., Oriental Mindoro Prov.; 13°07′N, 121°19′E; collected 15 Mar. 1937 by F. S. Rivera (see Barbour, 1939, p. 26); MCZ, 1. *Mfp*; *14.*

Patoc Barrio, Dagami Munic.; Leyte I., Leyte Prov.; 11°05′N, 124°52′E; collected 25–29 July 1961 by G. Alcasid and M. Celestino; AMNH, 2. *Mfp*; *62.*

Patok, Bo. See Patoc Barrio.

Pinamalayan; Mindoro I., Oriental Mindoro Prov.; 13°02′N, 121°29′E; collected 9 Mar. 1937 by F. S. Rivera (see Barbour, 1939, p. 26); MCZ, 3. *Mfp*; *13.*

Port Banga. See Banga, Port.

Port Princesa. See Puerto Princesa.

Puerto Princesa; Palawan I., Palawan Prov.; 9°44′N, 118°44′E; collected 22 ?Feb. 1887, 23 July 1887 by C. C. Platen (see Blasius, 1888, p. 302); RMNH, 1 (skin only); ZMB, 1 (skin only). *Mfp*; *5.*

Puerto Princesa area; Palawan I., Palawan Prov.; ca. 9°44′N, 118°44′E; collected July–Aug. 1874 by J. B. Steere (see Sharpe, 1876, p. 297; Günther, [1877], p. 735); museum unknown. *Mfp*; *5.*

Puerto Princesa, E, sea level; Palawan I., Palawan Prov.; ca. 9°44′N, 118°44′E; collected 9 Mar.–14 Apr. 1947 by H. T. Wright, C. F. Wally, and J. A. McCorkle (see Hoogstraal, 1951, p. 73); FMNH, 3; PNM, 1 (skin only; some postcranial bones in FMNH); FMNH (skull), PNM (skin, postcranial skeleton), 1. *Mfp*; *5.*

Puerto Princesa, "Mt. wooded area"; Palawan I., Palawan Prov.; 9°44′N, 118°44′E; collected 21 May 1965 by R. E. Kuntz; USNM, 1. *Mfp*; *5.*

Pulunbato, Mount, near; Mindanao I., Zamboanga del Sur Prov.; ca. 6°58′N, 122°05′E; collected 2–4 Feb. 1875 by H.M.S. Challenger Expedition (see Murray in Tweeddale, 1880, p. 7; Murray, 1885, p. 665; Swire, 1938, pp. 107, 110); BM(NH), 1. *Mff*; *117.*

Quezon National Park; Luzon I., Quezon Prov.; ca. 14°00′N, 121°45′E; reported by IUCN (1971, p. 392). *Mfp*; *27.*

Rio Grande. See Pulunbato, Mount.

Romblon I.; Romblon Prov.; 12°30′–12°35′N, 122°15′–122°20′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; *20.*

Samar I.; province unknown; 11°05′–12°40′N, 124°15′–125°45′E; captive albino presented 23 Apr. 1875 to Menagerie of Zoological Society of London by J. Ross (see Sclater, 1875, p. 349). Collected Apr. 1888 by J. B. Steere (1890, pp. 5, 28); museum unknown. Reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61; Worcester, 1898, p. 334). Reported as present 1894–1897 by J. Whitehead (in Thomas, 1898, p. 381). *Mfp*; see *54–57.*

Samboangan. See Pulunbato, Mount.

Sandayong, 300–350 m, Sierra-Bullones Munic.; Bohol I., Bohol Prov.; ca. 9°45′N, 124°20′E; collected Apr.–May 1955 by D. S. Rabor (pers. comm., 4 Aug. 1989; also see Rand & Rabor, 1960, p. 311), FMNH, 3 (skulls only). Subsp. indet.; *65.*

San Mariano Munic., Sierra Madre; Luzon I., Isabela Prov.; ca. 17°00′N, 122°00′E; collected in 1961 by American–Philippine Expedition; AMNH, 3. (For locality, see AMNH catalog, nos. 187083–187200.) Reported as prey of local Negritos, 1979–1980, by Rai (1990, pp. 28, 47, 182). *Mfp*; *44.*

San Nicolas, 6 km NE; Busuanga I., Palawan Prov.; ca. 12°04′N, 120°12′E; collected 23 May 1962 by M. Thompson (see BBM field catalog); USNM, 1 (skull only). Subsp. indet.; *11.*

San Pedro; Culion I., Palawan Prov.; 11°51′N, 120°01′E; collected 25–26 Mar. 1947 by D. S. Rabor (see Hoogstraal, 1951, p. 82); FMNH, 2; PNM, 3. *Mfp*; *9.*

San Ramon; Mindanao I., Zamboanga del Sur Prov.; 7°00′N, 121°55′E; collected 29 July 1929 by F. C. Wonder; FMNH, 5. *Mff*; *118.*

San Sebastian; Samar I., Western Samar Prov.; 11°43′N, 125°01′E; collected before 1888 by D.

Sánchez y Sánchez (see Gogorza y González, 1888, p. 255); specimen(s) in Museo de Ciencias naturales de Madrid (not seen). *Mfp*; *56.*

Santa Cruz; Luzon I., Cavite Prov.; ca. 14°15′N, 120°50′E; albino captive observed by R. P. Casto de Elera (1915, p. 34). *Mfp*; *31.*

Santa Cruz; Mindanao I. See Badiang, Matutungan, and Pantod, Mount.

Santa Maria; Mindanao I., Zamboanga del Norte Prov.; 7°45′N, 122°07′E; observed 17 Feb. 1904 by E. A. Mearns (unpubl. MS., USNM). *Mff*; *115.*

Sarangani Group. See Balut I.

Sayao, Mount; Biliran I., Leyte Prov.; 11°33′N, 124°29′E; collected 27 Apr. 1987 by E. A. Rickart; USNM, 1 (skull only). Probably *Mfp*; *59.*

Siargao I. monkeys not included in mammalian faunal list published by L. R. Heaney and D. S. Rabor (1982, p. 16). Not mapped.

Siaton, 10 km N; Negros I., Negros Oriental Prov.; ca. 9°09′N, 123°02′E; collected 26 July ?1962 by ?D. S. Rabor; museum unknown (data from BBM field catalog). *Mff/Mfp 76.*

Sibutu town; Sibutu I., Tawitawi Prov.; 4°50′N, 119°27′E; no monkeys seen 7 Jan. 1906 by E. A. Mearns (unpubl. MS., USNM). Not mapped.

Sibuyan I.; Romblon Prov.; 12°15′–12°30′N, 122°25′–122°45′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; see *21.*

Sierra Bullones. See Cantaub and Sandayong.

Sierra Madre. See Dimalasud Barrio and San Mariano Munic.

Sigayan, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 23 May–5 June 1950 by D. S. Rabor; FMNH, 5. *Mff*; *110.*

Siquijor I.; Siquijor Prov.; 9°05′–9°20′N, 123°25′–123°40′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Probably *Mff/Mfp*; *81.*

Situbo, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 22–26 May 1950 by D. S. Rabor; FMNH, 5. *Mff*; *110.*

Sohoton Natural Bridge National Park; Samar I., Western Samar Prov.; ca. 11°30′N, 125°08′E; reported by IUCN (1971, p. 389). *Mfp*; *57.*

South Coast Range. See Arubal River, Banganan River, and Nituna River.

Sulu. See Crater Lake Mountain and Jolo.

Sulug. See Sumlog River.

Sumlog River, mouth; Mindanao I., Davao Oriental Prov.; 6°53′N, 126°02′E; collected 12 June 1904 by E. A. Mearns; USNM, 1. *Mff/Mfp*; *92.*

Surigao, immediate vicinity; Mindanao I., Surigao del Norte Prov.; ca. 9°45′N, 125°30′E; collected May 1877 by A. Everett (in Günther, 1879, p. 74); BM(NH), 1. No monkeys seen Apr. 1904 by E. A. Mearns (unpubl. MS., USNM). *Mfp*; *82.*

Sutug River. See Sumlog River.

Tablas I.; Romblon Prov.; 12°05′–12°40′N, 121°55′–122°10′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Subsp. indet.; *19.*

Tacuta, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 4 June 1950 by D. S. Rabor; FMNH, 3. *Mff*; *110.*

Tagabli. See Pantod, Mount.

Tagabuli. See Badiang, Matutungan, and Pantod, Mount.

Tagulaya River, left bank, 650 ft (= 200 m); Mindanao I., Davao Oriental Prov.; ca. 6°55′N, 125°27′E; observed 15 June 1904 by E. A. Mearns (unpubl. MS., USNM). *Mff/Mfp*; *93.*

Talinis, 3500 ft (= 1000 m); Negros I., Negros Oriental Prov.; ca. 9°21′N, 123°03′E; collected 5 Dec. 1953 by A. L. Rand (unpubl. sketch map and notes, FMNH); FMNH, 6. *Mff/Mfp*; *78.*

Tampalan, Katipunan Munic.; Mindanao I., Zamboanga del Norte Prov.; not precisely located, ca. 8°30′N, 123°15′E; collected 4 June 1950 by D. S. Rabor; FMNH, 1. *Mff*; *110.*

Tangob. See Tangub.

Tangub, near, Panguil Bay, 20 ft (= 6 m); Mindanao I., Misamis Occidental Prov.; 8°03′N, 123°44′E; collected 9 May 1906 by E. A. Mearns (unpubl. MS., USNM; also see Rand & Rabor, 1960, p. 262); USNM, 2 (1 skull only). Probably *Mff/Mfp*; *107.*

Tarabanan, Concepcion Barrio, Puerto Princesa region; Palawan I., Palawan Prov.; ca. 10°01′N, 119°02′E; collected 14–15 May 1962 by D. S. Rabor (see Kuntz, 1969, p. 208); USNM, 2. *Mfp*; *6.*

Tawitawi I.; Tawitawi Prov.; 5°05′–5°20′N, 119°45′–120°15′E; reported as present 1890–1893 by F. S. Bourns and D. C. Worcester (1894, pp. 6, 61). Living captives obtained 16 Feb. 1987 and 20 Mar. 1987; SICONBREC, 2 (captives examined 4 Aug. 1989). *Mff*; *127.*

Terabanon. See Tarabanan.

Tiputipu. near; Basilan I., Basilan Prov.; ca. 6°30′N, 122°04′E; observed 2 Feb. 1906 by E. A. Mearns (unpubl. MS., USNM). *Mff*; *124.*

Tolong. See Balangbang, Kandomao, and Naliong.

Tuy; Luzon I., Batangas Prov.; 14°01′N, 120°44′E; collected before 1888 by D. Sánchez y Sánchez (see Gogorza y González, 1888, p. 255); specimen(s) in Museo de Ciencias naturales de Madrid (not seen). *Mfp*; *30*.

Upi. See Burungkot.

Viritar. See Laoag, N.

Zambales Prov.; Luzon I.; 14°45′–15°50′N, 119°50′–120°30′E; laboratory animals obtained 1960–1969 by Virus Laboratory of Institute of Public Health, University of Philippines, Manila (Famatiga, 1973, p. 316); apparently not preserved. *Mfp*; *40*.

Zamboanga; Mindanao I., Zamboanga del Sur Prov.; ca. 6°54′N, 122°04′E; collected 13–19 June 1861 by E. von Martens (1876, pp. 193, 206, 362) and Herr Pieschel; ZMB, 1 (skull only; series originally also included 3 skins). Collected 23 Mar.–11 Apr. 1906 by L. Wood, Jr. and E. A. Mearns; USNM, 3. *Mff*; *117*.

Zamboanga area; Mindanao I., Zamboanga del Sur Prov.; ca. 6°54′N, 122°04′E; collected Sep.–Nov. 1874 by J. B. Steere (see Sharpe, 1876, p. 297; Günther, [1877], p. 735); museum unknown. *Mff*; *117*.

Zamboanga del Norte Prov. or Zamboanga del Sur Prov.; Mindanao I.; 6°55′–8°45′N, 121°55′–123°40′E; laboratory animals obtained 1960–1969 by Virus Laboratory of Institute of Public Health, University of Philippines, Manila (Famatiga, 1973, p. 316); apparently not preserved. *Mff*; see *110–119*.

Zamboanga del Sur Prov.; Mindanao I.; 6°55′–8°20′N, 121°55′–123°40′E; captive acquired 30 Mar. 1987; SICONBREC, 1 (captive examined 4 Aug. 1989). *Mff*; see *113, 114, 116–119*.